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Age, Rate of Growth, and General Life-history of the Australian Pilchard (*Sardinops neopilchardus*) in New South Wales Waters

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FOREWORD

The waters surrounding the island-continent of Australia have been shown to contain thousands of different species of fish, of which relatively few are of commercial importance. One of the tasks of the C.S.I.R. Division of Fisheries is to increase this proportion by determining the occurrences of species not yet utilized to any considerable extent, and above all, to determine how reliable in occurrence the more promising species are. There are often great variations from year to year in the resultant productivity of spawning seasons, and thus greatly varying accessions to the fish stocks occur. Another factor contributing to the ultimate weight of fish available for capture is the rate at which the fish grow, and this can vary also very considerably from region to region. Naturally, a fast growth-rate is desirable from the fisherman's standpoint.

Biological studies of this nature have been all too rare with respect to Australian fishes. This paper is one of a series designed to fill the gap as far as the Australian pilchard is concerned.

In most of the large fisheries of the world, foundation studies of this nature have followed upon the establishment of a commercial fishery and have had the disadvantage of dealing with fish stocks which have suffered alteration, and sometimes depletion, and are therefore not in their pristine condition; in this particular case the study has had the advantage of preceding the establishment of a fishery, but on that very account only limited material has been available on which to work.

The net result is a closely reasoned presentation of results which will doubtless be a useful guide to scientific workers in similar fields and to those who are now endeavouring to establish a fishery on pelagic fish, including the pilchard.

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SUMMARY

Studies of the age and growth rate of the unexploited pilchard of New South Wales were carried out by means of scale-readings and analysis of length-frequency distributions. In spite of shortages of material for both purposes, and some special difficulties connected with the scales, a very consistent set of results was obtained. It is shown in particular that the fish measure about 4·2, 5·6, 6·6, and 7·5 inches in mean total length at ages of about $1\frac{1}{4}$, 2, 3, and 4 years, and that most of the growth in each year probably occurs in the spring and summer.

The general scheme of the life-history is outlined. The pilchards hatch at sea but assume an inshore phase very soon afterwards. This lasts until they are over a year old when the fish return to the sea and remain there. A substantial proportion of them mature at two years of age, and nearly all are ripe at three.

In growth-rate and in the general life-history, the New South Wales pilchard resembles that of the Atlantic coasts of south-western Europe more than it does the other closely related pilchard groups that have been studied elsewhere.

The scale material presented some rather complex problems which seem to have received insufficient attention elsewhere, and which are discussed in the paper. Special attention has been paid to differences in the appearance of age-rings, and to their significance.

The Age, Rate of Growth, and General Life-History of The Australian Pilchard (*Sardinops neopilchardus*) in New South Wales

I. INTRODUCTION

1. Circumstances of the Study

In 1937 the writer was assigned the task of conducting biological investigations upon the virtually unexploited Australian clupeoid fishes. There are some 40 species recorded from these waters, and at that time practically nothing was known about any of them beyond the usual taxonomic descriptions, some notes on the juvenile stages of one or two forms, and some information (mostly very incomplete) as to regional distribution.

Although the majority of these species are from the tropical waters, it was a logical first step to concentrate upon the dozen or so that were not, as being the closest to hand and the most likely to receive attention on the commercial side. For the first few years, therefore, there was a general effort to collect all the available information upon these, and a preliminary report was issued dealing with eight of them (Blackburn 1941). Since then it has become more clearly apparent that only two or three of these have any great potential importance at the present time, and the clupeoid research has been concentrated upon them.

The present paper deals mainly with the determination of age and growth rate in the pilchard in New South Wales waters, this being a necessary basis for studies on abundance fluctuations. Such investigations represent the main way in which research can be expected to assist any commercial fishery that may develop. In the meantime, a full knowledge of these matters, and of the life-history generally, is also helpful to those who are trying to develop such a fishery. At the end of the paper there is an outline of the general life-history of the fish. The work also serves to emphasize some matters that have received insufficient attention in most literature on age-studies with fishes.

2. Methods and Limitations

The three methods usually utilized in studies on age of fish have been employed in the present study, namely, the Petersen method (analysis of length-frequency distributions) and the scale and otolith methods (recognition of periodic structures in the discrete hard parts of the fish).

The present study deals specifically with pilchards from New South Wales waters, and the conclusions therefore do not necessarily apply to the fish from other parts of Australia. It has been pointed out before (Blackburn 1941, pp. 7, 30, 43) that there are strong reasons for believing that the pilchards of eastern Australia (New South Wales–Queensland) are distinct from those of southern Australia (Victoria–South Australia–Tasmania). Growth-rates might easily be

different in these two groups. Virtually no adult pilchard material has been obtained from Queensland, and thus the study of the eastern Australian fish had to be confined to those of New South Wales waters.

Even with the latter the material available for study was much less extensive than could have been wished. Virtually no pilchard fishery exists in this area, and most of the specimens were only secured by experimental fishing, mainly from the Council's vessel *Warreen*. Since this work has never been on a large scale or even regular in any way, owing to difficulties with the fishing methods which have not yet been overcome, these limitations were unavoidable. The search for material was vigorously prosecuted in all possible directions, and even the stomach contents of larger fish were examined. Another difficulty was that many of the fish that were obtained had lost most of their scales in the nets. Nevertheless the amount of material used was as large as that of many other authors, and it is felt that the conclusions drawn from it are satisfactorily based.

The fish lengths referred to in this paper are body lengths, not total lengths, unless otherwise stated. The body length is the length excluding the caudal fin, and is measured in the manner of the Californian sardine investigators (loc, cit, p. 15). Where half-centimetre size-groups are mentioned, 10·0 cm. means 100 to 104 mm., and 10·5 cm. means 105 to 109 mm., for example.

II. STUDIES WITH THE PETERSEN METHOD

The total number of fish measured, excluding larvae taken in plankton nets, was 10,124. These were from 83 samples, of which there were 1 each in 1936 and 1938, and 22, 44, and 15, respectively in 1939, 1940, and 1941. Details of these are given in Table 1. Length-frequency polygons have been prepared separately for the data of each of the latter three years and for the total of those over the whole period of investigation (Fig. 1). Yearly samples were employed because all the different age-groups would not be represented in samples from any more restricted periods of time. In the material available for this study the 0– and I–group pilchards were mainly taken in the spring and summer, and the older groups in the autumn and winter. The data of Table 2, in which the total of measured fish is analysed by half-centimetre groups and by seasons, demonstrate this very clearly. The 0– and I–group fish may be taken, by reference to Fig. 1, as all those under 11·0 cm. in length, and the older fish as all of that size or over. Of the former, Table 2 shows that the numbers taken in the different seasons were:

Spring	2,662	Combined	3,911
Summer	1,249		
Autumn	101	Combined	103
Winter	2		
Total:	4,014		4,014

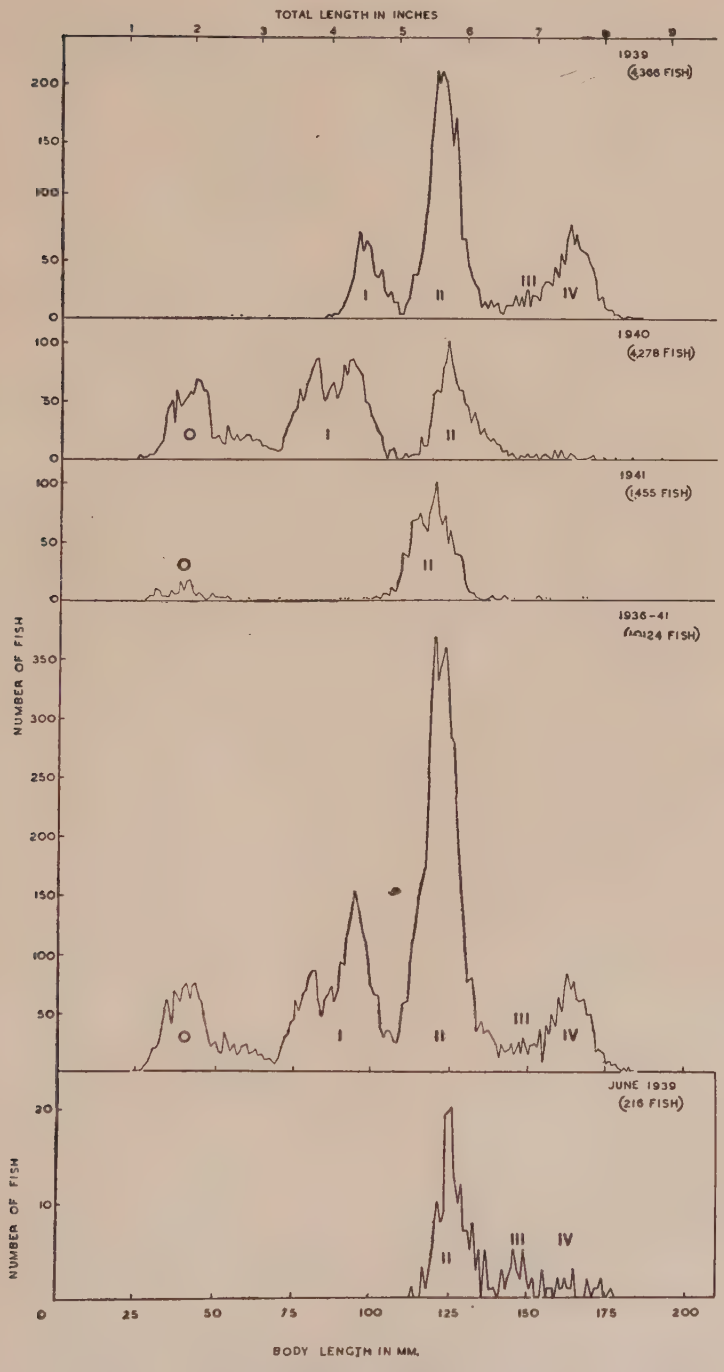

Fig. 1.—Length frequency polygons for New South Wales pilchards, taken in the years 1939, 1940, and 1941; during the entire period of investigation, 1936-1941; and in June, 1939.

That is to say, 97·4 per cent. of the fish of the two younger groups were obtained in the spring and summer. For the older ones, the position is:

Spring	252	Combined	529
Summer	277		
Autumn	3,696	Combined	5,581
Winter	1,885		
Total:	6,110		6,110

The situation here is practically the opposite to that above, 91·3 per cent. of individuals representing autumn and winter captures.

This is important because it shows that the intervals between the I– and II–group modes in these yearly polygons cannot represent annual increments of length. It also suggests that the same might even be true of the intervals between some of the other pairs of adjacent modes. It is shown in the next section that the spring and summer is a period of fast growth for at least the I–group fish, so it is quite likely that the intervals between the 0– and I–group modes are not strictly annual. On the other hand, it also appears that the autumn and winter is a season of very slow growth for the older fish, and so the position of the modes of these groups is probably not seriously affected by any question of time of measuring in the whole six months' period, and the intervals between adjacent pairs could be regarded as typical annual increments of length.

As the sampling of these fish was unavoidably inadequate, the yearly polygons in Fig. 1 cannot be considered to represent the actual age-composition of the species in those particular years, or in any years. This sampling difficulty is the cause of many omissions and some apparent anomalies in this part of the work, and it is difficult to present a convincing picture of what is probably a very simple and typical situation. From Fig. 1 most fisheries workers would not hesitate to identify separate age-groups with modes at about 41-44, 82-95, 120, and 163 mm., respectively. They would probably look for another between the last two, and subsequent scale work has shown that this exists, but it is not obvious because of the uneven sampling. Apparently fish of this group were taken in appreciable numbers in 1939 only, and even in the sample of that year their status is obscured because of the much greater numbers in the two adjacent groups. Only upon reference to a separate length-frequency distribution, for material of June 1939, is the situation in any way clearly revealed, and even in that case the demonstration is far from ideal because of an unfortunately small number of fish (Fig. 1).

Admitting the occurrence of this group, the identification of the various age-groups is not difficult. The fish of the group with modal length between 40 and 45 mm., must be either about six or eighteen months old, because the principal spawning season in these waters is from the late autumn to early spring (Blackburn 1941, pp. 34-5, 39, 43). Obviously the former is the more likely, and in any case some of the smaller fish have definite post-laval characters (loc. cit., pp. 22-3). This is then the 0-group. The next group, with modal length between 80 and 95 mm., are also spring and summer fish.

TABLE 1

DETAILS OF NEW SOUTH WALES PILCHARD SAMPLES

(*Note:* Locality names followed by (S) are sea localities for purposes of Table 2; all others refer to bays. Samples indicated * in the first column are those from which some scales were available)

Date	Locality	Number Measured	How Procured
3·x·36	Pittwater	21	(From Professor W. J. Dakin)
3·ii·38	Middle Harbor	4	(From N.S.W. Fisheries Dept.)
*13·iv·39	Port Hacking	5	Beach seine
14·iv·39	Port Hacking	1	Hook
18·iv·39	Brush Island (S)	1	*Ex* bonito
*10·v·39	Off Botany Bay (S)	1	Trawl
*12·v·39	Port Jackson	33	Beach seine ? (market)
*17·v·39	Off Port Stephens (S)	2,405	Hoop net
*18·v·39	Port Jackson	2	Beach seine ? (market)
*21·vi·39	Red Head (S)	13	Dip net
*24·vi·39	Camden Head (S)	28	*Ex* mackerel tuna
*25·vi·39	Bird Island (S)	5	*Ex* mackerel tuna
*26·vi·39	Bird Island (S)	170	Hoop net
*9·viii·39	Cape Hawke (S)	789	Hoop net
13·viii·39	Off Richmond River (S)	8	*Ex* mackerel tuna
18·viii·39	Port Jackson	9	? (market)
24·viii·39	Off Jervis Bay (S)	1	*Ex* john dory
1·ix·39	Port Jackson	6	? (market)
5·ix·39	Port Jackson	5	? (market)
8·ix·39	Port Jackson	6	? (market)
14·ix·39	Port Jackson	182	? (market)
*16·x·39	Wagonga Inlet	2	Beach seine
1·xi·39	Tollgates Island (S)	3	*Ex* southern bluefin
*21·xi·39	Wagonga Inlet	691	Beach seine
*15·i·40	Port Stephens	6	Drift net
19·i·40	Nambucca River	210	Beach seine
*20·i·40	Off Port Stephens (S)	5	Drift net
22·i·40	Off Port Stephens (S)	261	Drift net
11·ii·40	Jervis Bay	69	Lampara
*24·iv·40	Off Port Stephens (S)	79	Drift net
5·vi·40	Jervis Bay	250	Lampara
*12·vi·40	Twofold Bay	7	*Ex* salmon
*17·vii·40	Twofold Bay	1	Dip net
*30·vii·40	Tacking Point (S)	3	*Ex* gannet
*31·vii·40	Off Camden Haven (S)	600	Lampara
*2·viii·40	Off Broken Bay (S)	1	*Ex* striped tuna
*17·ix·40	Middle Harbor	7	Beach seine
18·ix·40	Off Twofold Bay (S)	13	*Ex* flathead
*26·ix·40	Bateman's Bay	14	Hoop net
*26·ix·40	Twofold Bay	78	Hoop net
27·ix·40	Tathra to Merimbula (S)	11	*Ex* southern bluefin
30·ix·40	Jervis Bay	4	Hoop net
*5·x·40	Bateman's Bay	171	Hoop net
5·x·40	Jervis Bay	1	*Ex* bonito
*6·x·40	Tathra to Merimbula (S)	9	*Ex* southern bluefin
*6·x·40	Off Bermagui (S)	7	*Ex* southern bluefin
*6·x·40	Off Merimbula (S)	1	*Ex* bonito
*7·x·40	Jervis Bay	6	*Ex* gannet
*7·x·40	Jervis Bay	14	Dip net
8·x·40	Jervis Bay	1	Dip net
*9·x·40	Twofold Bay	4	*Ex* salmon
10·x·40	Port Stephens	518	Hoop net
12·x·40	Montague Island (S)	6	*Ex* southern bluefin
*12·x·40	Twofold Bay	6	Dip net
13·x·40	Montague Island (S)	8	*Ex* southern bluefin
*25·x·40	Jervis Bay	951	Lampara

TABLE 1—*continued*

Date	Locality	Number Measured	How Procured
*1·xi·40	Brush Island (S)	1	*Ex* southern bluefin
4·xi·40	Brush Island (S)	1	*Ex* southern bluefin
*5·xi·40	Twofold Bay	2	Dip net
*6·xi·40	Twofold Bay	7	Dip net
14·xi·40	Off Bateman's Bay (S)	1	*Ex* southern bluefin
*19·xi·40	Twofold Bay	78	Hoop net
27·xi·40	Jervis Bay	36	Lampara
*28·xi·40	Twofold Bay	1	Dip net
29·xi·40	Montague Island (S)	1	*Ex* southern bluefin
*1·xii·40	Jervis Bay	13	Dip net
*8·xii·40	Jervis Bay	812	Lampara
*18·xii·40	Twofold Bay	3	*Ex* salmon
—·i·41	Wreck Bay (S)	4	(From skipper, *Helen Dawn*)
*12·i·41	Twofold Bay	120	Hoop net
*27·ii·41	Twofold Bay	14	Hoop net
27·ii·41	Twofold Bay	1	Hoop net
22·iv·41	Jervis Bay	712	Lampara
23·iv·41	Jervis Bay	558	Lampara
6·vi·41	Port Jackson	1	? (market)
*21·vi·41	Cape Howe (S)	1	*Ex* southern bluefin
11·x·41	Montague Island (S)	8	*Ex* bonito
11·x·41	Montague Island (S)	3	*Ex* southern bluefin
*7·xi·41	Twofold Bay (S)	11	*Ex* southern bluefin
8·xi·41	Twofold Bay (S)	3	*Ex* southern bluefin
9·xi·41	Twofold Bay (S)	1	*Ex* southern bluefin
*9·xi·41	Twofold Bay (S)	14	*Ex* southern bluefin
22·xii·41	Off Coogee (S)	4	*Ex* salmon
	Total	10,124	

and so they are mostly about a year older than the first group, i.e. about fifteen to eighteen months old, and the group itself is the I–group. The following one is much more regular, the mode only varying between about 120 and 125 mm. This is the II–group, but as shown above, the material was taken in the autumn and winter and thus the average age is about two years. The general season of capture of practically all the larger pilchards is virtually the same as in this case, and so the following age-group contains the three-year-olds and the next one those at about four years. These are the III– and IV–groups, with modes of about 150 (very approximately) and 160 to 165 mm. respectively. A few larger individuals up to 193 mm. in length, occurred in these samples, and these were probably five or six years old. More recently a pilchard measuring 196 mm. in body length, or just 9 inches in total length, was taken in New South Wales.

Studies of modal progression with time are particularly useful to demonstrate the actual age-group character of the peaks in the length-frequency polygons, and also to indicate changes in growth-rate at different seasons. It is usual to utilize a series of such polygons representing the successive months of some specific year or longer period, but in this case it was impossible to do so. In the period of these investigations there were many months in which no fish came to hand at all, and many also in which they were too few to show even one well-defined age-group. Therefore a series of length-frequency polygons is presented for all the data of the different months of the year irrespective of the actual years in which they became available, and even adopting this procedure the picture is incomplete, because no fish were taken in March in any year.

TABLE 2

N.S.W. PILCHARDS, ALL RECORDED SPECIMENS, 1936-41. DISTRIBUTION BY SIZE, SEASON, AND ENVIRONMENT (BAY OR SEA)

Body Length (cm.)	Spring					Summer					Autumn					Winter					Total				
	Total	Bay		Sea		Total	Bay		Sea		Total	Bay		Sea		Total	Bay		Sea		Total	Bay		Sea	
	No.	No.	%	No.	%	No.	No.	%	No	%	No.	No.	%	No.	%	No.	No.	%	No.	%	No.	No.	%	No.	%
2·5	1	..	..	1	100	17	17	100	..	..	..	..	..	..	..	..	..	..	..	..	18	17	94	1	6
3·0	31	14	45	17	55	125	125	100	..	..	..	..	..	..	..	..	..	..	..	..	156	139	89	17	11
3·5	104	82	79	22	21	187	187	100	..	..	..	..	..	..	..	..	..	..	..	..	291	269	92	22	8
4·0	279	272	97	7	3	74	74	100	..	..	..	..	..	..	..	..	..	..	..	..	353	346	98	7	2
4·5	193	193	100	..	..	14	12	86	2	14	..	..	..	..	..	1	1	100	..	..	208	206	99	2	1
5·0	98	96	98	2	2	10	10	100	..	..	3	3	100	..	..	..	..	..	..	..	111	109	98	2	2
5·5	90	86	96	4	4	..	..	..	..	..	1	1	100	..	..	..	..	..	..	..	91	87	96	4	4
6·0	81	76	94	5	6	1	1	100	..	..	..	..	..	..	..	..	..	..	..	..	82	77	94	5	6
6·5	48	47	98	1	2	..	..	..	..	..	1	1	100	..	..	..	..	..	..	..	49	48	98	1	2
7·0	126	123	98	3	2	1	1	100	..	..	..	..	..	..	..	..	..	..	..	..	127	124	98	3	2
7·5	285	282	99	3	1	1	1	100	..	..	..	..	..	..	..	..	..	..	..	..	286	283	99	3	1
8·0	347	347	100	..	..	8	8	100	..	..	..	..	..	..	..	..	..	..	..	..	355	355	100	..	..
8·5	220	220	100	..	..	99	98	99	1	1	..	..	..	..	..	..	..	..	..	..	319	318	100	1	..
9·0	214	214	100	..	..	341	339	99	2	1	..	..	..	..	..	..	..	..	..	..	555	553	100	2	..
9·5	324	323	100	1	..	269	268	100	1	..	1	1	100	..	..	..	..	..	..	..	594	592	100	2	..
10·0	164	161	98	3	2	86	86	100	..	..	16	11	69	5	31	1	..	..	1	100	267	258	97	9	3
10·5	57	52	91	5	9	16	15	94	1	6	79	62	78	17	22	..	..	..	..	..	152	129	85	23	15
11·0	17	14	82	3	18	13	2	15	11	85	401	261	65	140	35	7	3	43	4	57	438	280	64	158	36
11·5	6	6	100	..	..	66	1	2	65	98	891	353	40	538	60	71	11	15	60	85	1,034	371	36	663	64
12·0	1	1	100	..	..	96	1	1	95	99	1,330	364	27	966	73	302	11	4	291	96	1,729	377	22	1,352	78
12·5	2	..	..	2	100	42	..	..	42	100	726	200	28	526	72	324	35	11	289	89	1,094	235	22	859	78
13·0	3	..	..	3	100	9	..	..	9	100	164	32	20	132	80	175	84	48	91	52	351	116	33	235	67
13·5	4	1	25	3	75	5	..	..	5	100	57	8	14	49	86	100	70	70	30	30	166	79	48	87	52
14·0	4	1	25	3	75	..	..	..	..	..	37	5	14	32	86	48	28	58	20	42	89	34	38	55	62
14·5	6	6	100	..	..	4	1	25	3	75	45	1	2	44	98	45	6	13	39	87	100	14	14	86	86
15·0	26	24	92	2	8	5	1	20	4	80	26	5	19	21	81	56	7	12·5	49	87·5	113	37	33	76	67
15·5	41	38	93	3	7	16	4	25	12	75	8	2	25	6	75	129	2	2	127	98	194	46	24	148	76
16·0	58	57	98	1	2	18	..	..	18	100	9	..	..	9	100	249	8	3	241	97	334	65	19	269	81
16·5	48	44	92	4	8	2	..	..	2	100	2	1	50	1	50	251	1	..	250	100	303	46	15	257	85
17·0	22	20	91	2	9	1	..	..	1	100	..	..	..	..	..	107	..	..	107	100	130	20	15	110	85
17·5	10	9	90	1	10	..	..	..	..	..	..	..	..	..	..	20	1	5	19	95	30	10	33	20	67
18·0	2	1	50	1	50	..	..	..	..	..	..	..	..	..	..	1	..	..	1	100	3	1	33	2	67
18·5	1	1	100	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	1	100	..	..
19·0	1	1	100	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	1	100	..	..
Total	2,914	2,812	96	102	4	1,526	1,252	82	274	18	3,797	1,311	35	2,486	65	1,887	268	14	1,619	86	10,124	5,643	56	4,481	44

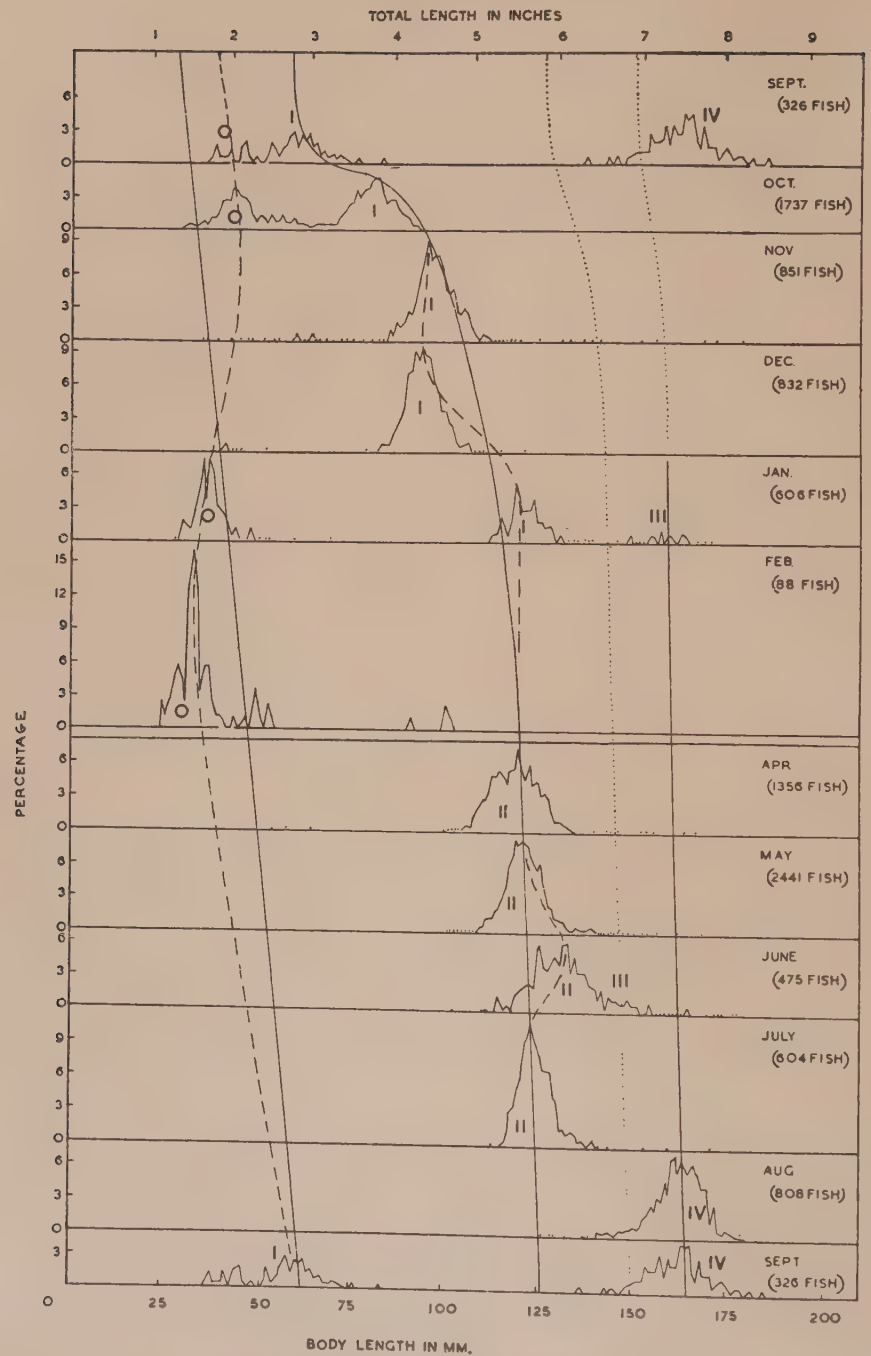

Fig. 2.—Length-frequency polygons for New South Wales pilchards taken in the successive months of the year (all years combined) during the period of investigation 1936-1941, and illustrating progression of the age-group modes. For further explanation see text.

Fig. 2 shows this series of polygons. The top (September) polygon is repeated at the bottom to preserve continuity in the diagram, and the length frequencies are expressed as percentages. The information conveyed is limited and its interpretation is difficult, this being due largely to the inadequacy of sampling and the grouping of material of different years. However, the writer feels that his interpretation of the data, as indicated by the lines joining the age-group modes, is sound. The suggested general sequence up to the second anniversary of birth is fairly convincing, and with this as a guide (particularly as to differing growth-rates by season) the further growth of the fish has been outlined in a reasonable manner. Indeed, there is no other satisfactory way of interpreting the available data.

It will be noticed that there is no very regular progression about the O-group data for the months September to February. The range of modal size for the whole period is from 33 to 43 mm., with 38 mm. as the middle of the range. The main spawning season for New South Wales pilchards is from about late autumn to early spring, although there is actually some spawning at all seasons; thus even in September there would be some fish of the current brood not hatched, whereas the September polygon in the figure under discussion shows that there can also be individuals of the same season's spawning available with modal size 38 mm. That is to say, there may be a difference of the order of 40 mm. in the size of the young of the same year during the actual spawning season itself, those hatched very early attaining this size by the end of the season, at the time others are only just appearing. This by itself is sufficient to explain the haphazard distribution of the modes in this case, for a period of time so soon after the season of origin. The larger September and October individuals in these samples would have been spawned at the beginning of the previous spawning period and the smaller January and February fish probably at the very end. If one were to ignore the small differences in these modal lengths during this six-monthly period, September to February, then, bearing in mind that the main season is also of approximately six months duration, it could be stated that:

Fish spawned in April–May grow to modal size 33–43 mm. by September.
Fish spawned in May–June grow to modal size 33–43 mm. by October.
Fish spawned in June–July grow to modal size 33–43 mm. by November.
Fish spawned in July–Aug. grow to modal size 33–43 mm. by December.
Fish spawned in Aug.–Sept. grow to modal size 33–43 mm. by January.
Fish spawned in Sept.–Oct. grow to modal size 33–43 mm. by February.

That is to say the average length attained by the fish at the age of about four to five months is in the vicinity of 38 mm., and at least some closely similar rate of growth is very clearly indicated. Fish hatched in mid-winter would reach this average size about November-December, and the growth of these young individuals has been indicated on this basis in Fig. 2.

There are virtually no data in these samples for the following six months that could be taken to represent the same hypothetical brood of fish, so the seasonal rate of growth at this stage of life, i.e. the first winter after hatching, cannot be demonstrated. It could quite easily be a continuation of the previous rate as is clear from the diagram, and it has tentatively been indicated as such,

but the position could well be otherwise. Incidentally, this and most of the other major gaps in the seasonal sequence of the material represent different phases in the life-history in which the fish are less available for catching than at other times, as explained later in the full account of the life-history: the only important break in this diagram for which this was not so is that for the III-group in the winter-time, whose under-representation in these samples is a real sampling "accident". The individuals of modal length about 60 mm. in the September polygon certainly represent the above-mentioned brood at an older stage, now the I-group. From this stage to the following July the material is better, and the growth of these I-group pilchards can be traced fairly convincingly throughout this period, to the stage at which they become the II-group at about 125 mm. modal length. The fast growth begins in October and ends probably about February or March. At least from April onwards there is virtually no increase in size at all.

Beyond this stage the evidence of the monthly samples is fragmentary. It is assumed that the general growth-rate pattern of the second year of life, i.e. with fast growth in the spring and summer and slow growth in the autumn and winter, is repeated in each of the two succeeding years. Actually, it would be difficult to link up the available data on any other basis. The information on the IV-group suggests that the period of slow winter growth normally extends into September.

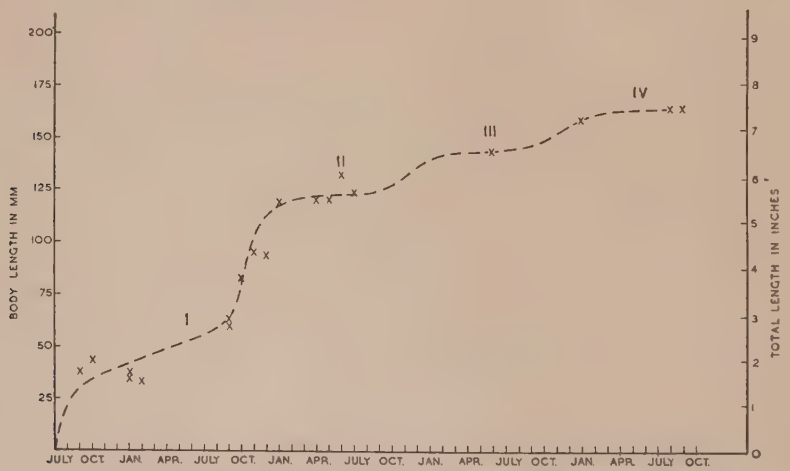

Fig. 3.—Scheme of general rate of growth of the New South Wales pilchard, from month to month and year to year, based on a study of progression of age-group modes in monthly samples. For further explanation see text.

The position is more clearly indicated in Fig. 3, using the same data. Group modal lengths have been plotted against the months in which they occur and a line fitted to indicate the probable scheme of growth, over four years, of a typical brood hatched in the middle of the spawning season. The flattened parts of the curve represent periods of slow winter growth (in the course of which the anniversaries of birth occur) and the steep parts, periods of fast spring growth. As indicated above, the position as regards growth-rate in the first winter after hatching is particularly uncertain.

The foregoing pages may be summarized as follows:

1. The pilchards of New South Wales grow to about 40 mm. in their first five months or so of life. The general size at the first winter after hatching, i.e. the first anniversary of birth for most, is not known, but is very likely about 55 mm.

2. From about the following October the yearlings grow rapidly until the mean length is about 120 mm., probably in about February-March.

3. In the second general winter season after hatching the growth is very slow, and the fish are thus about two years old when 125 mm. long. This period of slow growth begins in the autumn and probably extends to the early spring.

4. At their third and fourth anniversaries of birth the fish are about 150 and 160-165 mm. respectively in average length, though the former figure is very approximate. It is probable that there is fast growth in the spring and summer and slow growth in the autumn and winter in the third and fourth years, just as in the second.

5. Some fish live to greater ages than four years, perhaps to five or six, but these do not seem to be common.

III. STUDIES WITH THE SCALE METHOD

1. Introduction

(a) The Pilchard Scale and Annual Rings Described

The Australian pilchard scale is of the general clupeid type, as recognized by Cockerell (1913, pp. 123-5), Lee (1920, p. 4) and others. That is to say, it is cycloid, with the anterior (embedded) and posterior portions sharply differentiated; the former somewhat opaque, ornamented with numerous fine lines (striae) running more or less transversely, and also with a few much coarser transverse lines (radii); and the latter transparent, not ornamented, and smaller. It was described by Cockerell (1915, p. 36), and although portions of his description do not apply to all scales, it is unnecessary to go into details here, as the position is well enough shown by the photographs (Plates 1-7, and Plate 8, Fig. 1).

In Plate 1, Fig. 2, there is a light, narrow band inside the margin of the anterior (opaque) part of the scale, running continuously around the whole of this portion at approximately the same distance from the margin. A similar band or line may be seen in Plate 3, marked I in each figure. In Plate 7, Fig. 1, at least two such concentric lines marked II and III, may be fairly easily seen, and in Plate 7, Fig. 2, at least one, marked I. These are the clearest instances of complete typical annual rings in these photographs, which were selected to illustrate other features besides very good rings. Plate 2, Fig. 1, shows a case in which the transparent area of the ring seems to have invaded adjacent parts of the scale.

There are other complete rings in these figures that are not quite as clear at first sight. In Plate 6, Fig. 2, for example, ring III can be traced right around the opaque portion of the scale, although close to the apex it tends to appear as a dark rather than a light line. Ring IV in Plate 7, Fig. 1, rings III and IV in Plate 7, Fig. 2, and rings IV and V in Plate 8, Fig. 1, are all similar. Three concentrically arranged rings are also shown in Plate 6, Fig. 1.

Furthermore, there are similar markings which are clearly rings of the same type, but not completely visible all around the scale. Fairly obvious cases are Plate 2, Fig. 2 (I), Plate 3, Fig. 1 (II), Plate 6, Fig. 2 (II), and Plate 7, Fig. 1 (I), Plate 2, Fig. 2 (S), Plate 3, Fig. 1 (S), Plate 4, Fig. 1 (II), and Plate 8, Fig. 1 (III), are less clear, and Plate 3, Fig. 2 (II), Plate 4, Fig. 1 (I), Plate 4, Fig. 2 (I, II), Plate 7, Fig. 2 (II), and Plate 8, Fig. 1 (I, II), are extremely poor, but in all these cases sufficient of the appearance and position of the marks can be made out to make it fairly certain, by comparison with the better examples already noted, that they represent traces of annual rings. Only in Plate 1, Fig. 1, and Plate 5, Fig. 2, are no definite signs of any rings perceptible.

So far there has been demonstrated the existence of such lines on the anterior part of the scale only. However, in Plate 7, Fig. 2, ring III on the anterior part is continuous with a dark line running around the posterior transparent part of the scale. Other instances can be seen in the same figure (I) and in Plate 6, Fig. 1 (I), but with the mark on the posterior portion incomplete. In Plate 3, Fig. 2, a somewhat incomplete dark line on the posterior part will be accepted as a continuation of the (also incomplete) ring II on the anterior part. Obviously these rings are generally much less clearly marked on the posterior parts of the scales, although they are more regularly discernable than might appear from these figures. Indeed in a few cases the posterior sections of the rings have been clearer than the anterior sections, and have assisted in locating the latter, e.g. for ring II in Plate 3, Fig. 2.

Now these markings on the Australian pilchard scale resemble the proved annual rings described by numerous authors for the scales of various other clupeid fish, and it is for this reason that they are claimed at this stage as actual annual rings. It will be shown later to what extent this is so. Dahl (1907) was the first author to give a proper account of these transparent rings in a clupeid species, the Atlantic herring, *Clupea harengus,* and he was followed by a great number of authors, among them Lea (1919, pp. 82-92) on *C. harengus,* W. F. Thompson (1916, pp. 55-8) on the Pacific herring *C. pallasii,* and Robertson (1933) on *C. harengus* and the European sprat *C. sprattus.* Robertson paid special attention to the appearance of the rings on the posterior part of the scale, which it is clear from his paper are more or less similar to those occurring in this pilchard material; and as regards the anterior part, all authors find markings like those described above i.e. transparent lines or thin bands running more or less parallel to the margin of the scale and to one another. Species of pilchards (i.e. of the genera *Sardina* and *Sardinops*) show this in the same way as do the herrings, sprats, and others. This is clear from the works of numerous authors on the European *Sardina pilchardus,* which are listed and summarized by De Buen (1937, pp. 376-94); of Aikawa (1940) on the Asiatic *Sardinops melanosticta;* and of Walford and Mosher (1943*a*, 1943*b*) on *S. caerulea* of the North American Pacific coast. Judging from the literature, however, the rings in the Australian pilchard scales are on the whole much less distinct than in those of many other clupeids (e.g. *Clupea harengus*); though in some other species the scales seem no better, if not worse, in this respect (e.g. *Sardinops caerluea*).

The precise appearance of the transparent rings is a matter which has received some attention from workers on other clupeid species, and it has some interesting implications, as will appear later in this paper. There are

five factors which have been or could be put forward to explain the appearance of annual rings in clupeid scales. These are as follows:

1. The striae become fainter where they cross the positions of the rings. Dahl (loc. cit., p. 8) and with more reservation Lee (1920, p. 4) attributed the transparent rings of the Atlantic herring scale in part at least to this. Paget (1920, p. 18) found that a section of a scale of *Clupea reevesi* " shows the striae distinctly less perfectly developed as they pass over the ridge, though the actual deposit of the upper layer does not seem to be less ". However, Robertson (1933) apparently discounted this, and attributed the transparency of the rings in the herring and (especially) sprat scales to a combination of three other factors, viz.:

2. The striae are interrupted at the positions of the rings. Robertson apparently found this only close to the basal line, and not of special importance.

3. There are concentric folds on the scale surface corresponding to the positions of the rings, and owing to perspective the striae appear to bend or kink when crossing these folds, in such a way that they seem to become first relatively closely approximated to each other and then relatively widely separated, giving by contrast the effect of a transparent zone. This only takes place where the striae meet the folds at an acute angle, i.e. in the region of the shoulders of the rings.

4. The striae become successively approximated and divergent where they cross the positions of the rings, producing by contrast the same sort of effect as that just described, but apparently quite independently of the kinking of the striae and presumably for quite other reasons.

These four explanations bear upon the transparent appearance of the rings. However, it was noted previously that the rings in the Australian pilchard scales may also sometimes appear in part as dark zones. The writer has not seen this noted in any other clupeid scale study*. It seems to involve a fifth factor, viz.:

5. The parallel striae appear approximated along their length so as to give the effect of a dark line in the position of the ring. Obviously this could only occur in respect of such sections of the rings as were generally parallel to the striae, i.e. the sections between the shoulders and the apex, which is where it is found.

It is interesting to analyse the appearance of the rings on these pilchard scales, taken as a whole, to discover to what extent these five factors account for the appearance of the rings. Considering them separately, it is found that:

(i) There are very few cases of transparency due purely to faintness of the striae, and this factor seems quite unimportant. A few short tracts of the ring in Plate 1, Fig. 2, especially around the shoulders and thence to the basal line, show this formation.

* That is, in any study of typical clupeid scales as previously defined. However, W. F. Thompson (1916, p. 56) found that scales from the back of the Pacific herring have the striae more or less concentrically arranged, and exhibiting a ring structure similar to that now described, but developed all round the anterior part of the scale.

This concentric arrangement of the striae has also been found in the scales of the posterior part of the back of the Atlantic herring (Paget 1920, pp. 18-9), and in those of the caudal peduncle in the shad *Caspialosa saposhnikovi* (Tchougounova 1940, p. 34). It is also found in certain scales from the back of the Australian pilchard.

(ii) There are a great many cases of the interruption of the striae, and this is quite clearly by far the most important factor making for the appearance of the rings. Almost every ring illustrates this in at least some part of its length, the one in Plate 1, Fig. 2, being one of the rare exceptions. The sections of the ring in Plate 2, Fig. 1, from the shoulders to the basal line show an extreme development of this discontinuity; on the other hand, there are cases in which it is only visible with difficulty, e.g. the apical sections of the three rings in Plate 6, Fig. 1, and the apical and shoulder sections of ring IV in Plate 7, Fig. 2. More typical cases are the apical sections of the ring in Plate 5, Fig. 1, and the basal sections of all the rings in Plate 6 and Plate 7, Fig. 2. It appears that, while these breaks in the striae may occur at any part of a ring, they are more common and generally much better developed in the sections between the shoulders and the basal line.

(iii) There are several cases of the striae becoming bent or waved across the rings as described by Robertson, and apparently accounting for the transparency in these instances on the lines suggested by him. Incidentally this waviness of the striae at the rings was also noticed, not only by Lee (1920, p. 4) as Robertson noted, but earlier still by W. F. Thompson (1916, p. 55) in the Pacific herring. On the whole these cases are not as clear as in Robertson's sprat scales, owing to the relatively closer arrangement of the striae, but they are obvious enough in such cases as the apical and shoulder positions of the ring in Plate 1, Fig. 2, the same on ring I in Plate 3, Fig. 1, the left shoulder of ring I in Plate 3, Fig. 2 (a particularly good case), and part of the right shoulder of ring II in the same figure. Other cases are less clear, e.g. parts of the apical and shoulder sections of ring II in Plate 7, Fig. 1. The fact that this phenomenon seems to be confined to the shoulder and apical sections (at any rate in so far as it is a cause of transparency) is in line with Robertson's observation that it only occurs in those sections of the ring where the striae meet it at an acute angle; those sections being, in his scales, at the shoulder and thence some little distance in either direction towards the apex and basal line. In this material the scales are so shaped that those sections of the ring which are at an acute angle to the striae are less extensive, being practically only at the shoulders and parts of the more apical sections, and the fact that these are practically the only places where the transparency effect from the wavy striae is developed seems to confirm Robertson's notion of this phenomenon. This may be one of the reasons why the annual rings are often so much less clear in pilchard scales than in those of the herring and sprat.

(iv) One notices no definite instances of transparent effects due to differences of spacing of striae other than those just remarked.

(v) There are several cases of the more apical sections of rings showing up fairly distinctly as dark lines due to close approximation of striae along their lengths in the appropriate positions. This is particularly clear in ring III in Plate 7, Fig. 2, and is also visible in parts of rings I in Plate 3, Fig. 2, II and III in Plate 6, Fig. 2, III and IV in Plate 7, Fig. 1, IV in Plate 7, Fig. 2, and IV in Plate 8, Fig. 1. The effect can only occur, in clupeid scales, in any sections of rings which may be parallel with the striae, thus confining it here to that part of the ring between the shoulder and apex.

Hence it seems that the appearance of these rings in the pilchard scales is due principally to interruption of the striae (a transparent effect); to a much less extent to an apparent difference, due to perspective, in the spacing of the striae in adjacent areas (a transparent effect), and to an approximation of the striae along their length (an opaque effect); and to a negligible degree to faintness of the striae (a transparent effect).

It is, however, possible to analyse the matter more fully than this. In recent years, there has been a tendency for workers upon clupeid scales to look for consistent differences in the appearance of rings within the same species, with a view to relating such to differences of environment and to sexual condition: thus making fuller use of the scale as a register of the life-history of the fish. Two papers which bear upon one aspect of this subject are those of Zamakhaev (1940) and Tchougounova (1940); these authors both dealt with species of shad (*Caspialosa*) in the Caspian Sea.

From the descriptions and figures of both these authors, it is apparent that there are two main kinds of rings upon the shad scales. One kind generally has the appearance of the rings with kinked striae described by Robertson (Tchougounova, pp. 22, 30). In the other kind (Zamakhaev, p. 13): "The ring appears to cut into the surface of the scale and interrupts sharply the rows of striae, so that they have blunt, broken-off ends at the ring of break"; whilst other features are that (p. 14): "Beyond the 'ring of break', especially on the sides of the scale, there is a narrow bright stripe without striae. In some places wider stripes without striae are formed, or stripes with faintly visible and separated striae . . ." and also "In the new zone of growth beyond the 'ring of break' the direction (angle) of the striae is changed in some parts of the scale. These changes of direction of the striae are found almost always at the spots where the shoulders and sides meet. No such changes are observed on the sides. At the top of the scale they are observed when the scales are of irregular form but rarely in the normal type having axial symmetry." According to these authors, the rings of the first kind are (mainly) the true annual rings, there being one for each year of life. Those of the second kind are the spawning rings, which are formed one for each year after the fish attains sexual maturity. Thus in the later years of the shad's life there are two rings formed each year, but the spawning ring, being formed subsequent to the yearly ring, is superimposed upon it and generally obliterates it, at any rate along the sides; this type of mark is not as a rule continuous around the apical part of the scale. Tchougounova pointed out (p. 22) that there may be occasional breaks in the striae in the true yearly rings, but distinct from those in the spawning marks.

As a basis for later discussions in this paper, it is appropriate here to examine the present pilchard material to see if there are the differences in the rings that these workers found. Since there are few or no rings that are fully of the "kinked-striae" type, and on the other hand almost every ring has the striae interrupted in part, this task in not simple. Some scales do exhibit rings which are rather similar to the spawning rings described and illustrated by the above-mentioned authors, especially those in Zamakhaev's photographs 5, 9 and 10 (pp. 10-1). These rings II and III in Plate 6, Fig. 1, rings II and III in Plate 6, Fig. 2, rings III and IV in Plate 7, Fig. 1, rings

III and IV in Plate 7, Fig. 2, and rings IV and V in Plate 8, Fig. 1. As in the shad material, this formation is developed almost entirely on the sides of the rings, although the marks are joined across the apical portion to form a continuous ring in each case. The marks are mainly very sharp and distinct, and do appear to cut into the surface of the scale in a way which other rings, even those which involve interruptions to the striae, mostly do not. Further, there is immediately outside each mark some development of the sort of zone recognized by Zamakhaev, in which there is not only, as a rule, a short break in the striae, but also, beyond that, a region in which the striae are typically rather faint, relatively well separated, or markedly discontinuous with those inside the ring. This is shown rather well in ring III in Plate 6, Fig. 2 (at the left), in ring IV in Plate 7, Fig. 2 (at the left), and in rings IV and V in Plate 8, Fig. 1, but in ring III in Plate 7, Fig. 1, it is hardly visible.

However, there are also several rings in these scales which, though largely owing their appearance to interruptions in the striae, are definitely not of this type: these are both rings in Plate 2, Fig. 2, both in Plate 3, Fig. 1, both in Plate 4, Fig. 1, and the ring in Plate 5, Fig. 1. There are also a few rings which are somewhat intermediate between both these groups, as in ring I in Plate 3, Fig. 2, ring I in Plate 6, Fig. 1, the ring in Plate 2, Fig. 1, and ring I in Plate 7, Fig. 2.

If one now leaves out of account the rings of the definite " spawning-mark " type it is obvious that interruptions in the striae are of much less importance as a factor contributing to the appearance of rings generally. If the " intermediate " cases are left out of account also, it can be seen that the number of rings that owe their appearance mainly to breaks in the striae is no larger than, if as large as, the number of those that owe their appearance to other factors (waviness of the striae, mostly). It can also be seen (whether the " intermediate " cases are included or not) that where tracts of break in the striae do occur they are no longer especially conspicuous between the shoulders and the basal line. Thus it is because of the fairly heavy representation of " spawning-mark " rings that breaks are the most important factor in ring formation, and are most conspicuous towards the basal line in this material. It may be added that the opaque effect contributing to the appearance of some rings seems to be much more common in the " spawning-mark " rings than in the others. One now perceives the possibility of attempting to classify the rings of pilchard scales into two groups, on somewhat similar lines to those outlined in the work of Zamakhaev and Tchougounova, though with more difficulty and some doubtful cases. On the one hand, there is the " spawning-mark " type, most distinct on the sides, owing its appearance there almost entirely to a very sharp and characteristic type of interruption of the striae, and often completed in the apical part of the scale by an opaque effect of approximated parallel striae. On the other hand, there is a group of rings in which breaks and waviness of the striae are usually both present and contribute in much the same measure, considering the material as a whole, to the transparent appearance of the rings; these rings are mostly more distinct on the shoulder and apical regions of the scales. Then there is a small group of intermediate cases. The contrast between these kinds is well seen in Plate 8, Fig. 1, where rings I, II, and III are of the plain type and rings IV and V

of the " spawning-mark " type. Another such contrast is provided in Plate 6, Fig. 2, where ring III is duplicated in the apical part of the scale only; the outside mark in this region is clearly a continuation of the rest of the ring, which is the " spawning-mark " type, while the inner one almost certainly represents a ring of the plain type of which the side tracts are not visible. This is probably a case in which the spawning mark has obliterated a plain ring of the same year in the side regions of the scale*, which also occurs in the Caspian shad material (Zamakhaev, p. 17; Tchougounova, p. 31). Actually these writers state that the ordinary ring is generally completely obliterated, but occasionally part of it remains. This type of apical duplication of a ring has also been noticed in the scales of the European and Mediterranean pilchard, by Fage (1913, p. 322), Murat (1935, p. 125), and De Buen (1937, p. 381), and was styled " casquette " by the latter author†.

It is sufficient to leave this matter at this stage for the time, though one point which can be emphasized here is that there is no clear basis for distinguishing the S-rings from at any rate some of the I-rings, both of these falling into the same category. The annual rings I, II, III, IV, and V are, of course, respectively the first, second, third, fourth, and fifth annual rings; the S-rings are the " secondary " ones. The way in which these were identified is described subsequently.

(b) Techniques

The general technique of cleaning and mounting was based on that of Lea (1919, pp. 101-2) and Graham (1929*b*). The scales were left overnight in a 2 per cent. solution of sodium peroxide and then transferred to a 2 per cent. solution of sodium sulphite. They were then mounted on slides with a very little Mayer's albumen as an adhesive and using a fair pressure to flatten them permanently on to the glass surface. These made excellent dry mounts which rarely became detached.

Only seldom was there any attempt to mount more than one scale from the same fish. Usually all the scales of all fish of the same size in the same sample were pooled, and a few of the clearest ones mounted together. This procedure is not recommended, and should not have been followed in this case. For the study in question, it had the result that there was not as much material as could have been desired for comparisons of the ring-pattern on different scales of the same fish, and (more importantly) that most of the scales could not be referred to fish of known sex (or condition). Actually about 20 per cent. of the mounted sets of scales were identifiable as to sex.

For the general examination of the scales, and the recording of measurements pertaining to the rings and magnifications of the scales, the special projector-apparatus described by Kesteven and Proctor (1941) was utilized, with slight modifications. An important part of any such work is the recording of the dimensions of the scales at the time of formation of each ring, measured along some convenient axis or radius. It was found that the rings were

* The same thing can be seen in ring IV in Plate 7, Fig. 1.

† In another scale, not figured here, the spawning mark occurs *inside* the associated plain ring, but this condition is exceptional.

generally more complete towards the apices of the scales than elsewhere, and so the scale radius from the centre of the basal line to the anterior apex was chosen for the line along which to record these intermediate scale lengths.

The virtue of this apparatus is that the screen can be moved into such a position that in the image the length of the anterior part of the scale along the axis of reference is equal to the length of the fish from which it was taken. Thus the calculation of the intermediate lengths of the fish from the intermediate lengths of the scale (as by the simple-proportion formula of Lea) becomes unnecessary, and the scale lengths S_1, S_2, &c. as read off the millimetre grid on the screen are actually the required fish lengths L_1, L_2, &c. This information can be of use even when the simple-proportion formula does not apply. The machine also enables one to record, by reference to a metre-rule beneath the screen and an empirically prepared graph, the magnification of the scale image when the screen is in its final position. From this, one can calculate back to obtain the actual length of the anterior part of the scale.

(*c*) *The Part of the Body from Which the Scales are Taken*

In deciding from which part of the body of a fish to take scales for age-studies, four points may be considered. These are as follows:

1. Scales from some parts of the body may have the annual rings generally less distinct in some way than those from other parts. For example, Storrow (1915) found, in the European pilchard, that in scales from behind the anal fin origin the number of rings cannot generally be exactly determined at all.

2. Scales from some parts of the body may have more rings than those from other parts. Buchanan-Wollaston (1924) and Hodgson (1925, pp. 3-4) found that scales from the anterior part of the Atlantic herring quite often have more rings than scales from the same fish taken between the dorsal fin and the tail, above the middle line.

3. The calculation of the intermediate fish-lengths L_1, L_2, etc. from the observed intermediate scale-lengths S_1, S_2, &c. depends upon the possibility of demonstrating some type of regression relationship between these two dimensions, operative over most of the life of the fish. In this connection, the data from scales from some part of the body may lead to a more easily manageable type of equation (from the point of view of back-calculation) than those from other areas. For example, Lea (1910*), who was investigating the possibility of utilizing the direct proportion formula for the calculation of the intermediate lengths from age-rings in the Atlantic herring, found that, whilst this relation did not hold precisely for scales from any part of the body, it held most nearly in the case of scales under the posterior half of the dorsal fin. In the haddock (*Gadus aeglefinus*), H. Thompson (1923, p. 75) likewise found that this relation held most nearly for the largest scales on the flank, and thus preferred to use these.

4. The mean intermediate lengths L_1, L_2, etc. may tend to differ for scales taken from different parts of the body, even though the same back-calculation formula may be involved. For instance, Kaganovskaya (1937) found for the Asiatic pilchard, calculating by the direct proportion formula

* Not available to the writer; quoted in Graham (1929*a*, p. 14), Lea (1938, pp. 17-8), and elsewhere.

throughout, that these values were generally relatively low for scales taken below the dorsal fin and above the middle line, and relatively high for those near the tail, compared with those for scales from other parts of the body. For the shad, *Caspialosa saposhnikovi,* Tchougounova (1940, pp. 36-7) found, also using the direct-proportion formula throughout, that scales from the anterior and posterior parts of the body gave relatively low and relatively high intermediate lengths respectively, a conclusion somewhat similar to that reached for some other species (salmons, gadoids) by Dannevig and Höst (1931). These authors therefore chose scales from the part of the body from which the mean calculated intermediate lengths showed the least deviation from the grand mean intermediate lengths calculated from scales from all parts.

However, it is probable that these last two considerations should be regarded as less important than previously, now that it is being realized that the direct-proportion type of relationship is not of so general occurrence as was once thought, that there are other possible types of fish-length/scale-length connection which are quite manageable from the standpoint of back-calculation, and that it can be expected that some one of these can be utilized in respect of scales from almost any place on the body. Both these considerations, where they have arisen in the literature, seem to have been based upon the desire to employ the direct-proportion formula at any cost. In fact the discrepancies found between mean intermediate lengths from different parts of the body, as mentioned in (4) above, were probably due partly to forcing this formula into service for scales from all parts, when at best it was probably only approximately correct for those of one part, as seen in (3) above. However, in cases where proportional growth between fish and scale does seem to apply for all parts of the fish, it would be useful to determine the area where there was least variation from the grand means in the intermediate lengths, as was done by Kesteven (1942, pp. 39-40) for mullet (*Mugil dobula*). As will be seen subsequently, this condition did not apply for the Australian pilchard.

Hence, as the phenomenon mentioned in (2) above also did not seem to apply in this material, the only important consideration was (1) above, the relative clarity of the rings in different parts of the body. It was decided that from this standpoint the best scales were the large ones beneath the dorsal fin, taken at or a little below the middle of the flank, and these were used fairly consistently throughout the investigations. Occasionally, when few or none of these scales were available, they were taken from any closely adjacent region. In no case were they taken from any relatively remote area, i.e. from anywhere except this general subdorsal region.

This was much the same region as that preferred by Kaganovskaya (loc. cit.) for the Asiatic pilchard, though other workers on clupeid age-studies have chosen different places. The part just above the pectoral fin, or some closely adjacent region, seems to have been most employed. Several workers have selected their material from the middle of the flank, but apparently mostly at or above the middle line.

(d) The Relationship between Scale-length and Fish-length

It is now appropriate to discover if there is a relationship, expressible as an equation involving one or more constants, between the selected scale dimension and the length of the fish. For this part of the study there were

available measurements of all the scales examined, 1,133 in number (excluding damaged and regenerated ones), which were obtained as mentioned before (Section III. 1, *b*). However, for 191 of these scales the corresponding fish measurements were only recorded in half-centimetres, that is to say, not precisely enough for the present purpose. There thus remained 942 pairs of measurements (L and S) which could be used, and these were grouped according to half-centimetre intervals of L and mean values for L and S were computed for each group. The data are set out in Table 3. When these averages are plotted (Fig. 4) it is clear that a straight line can be fitted closely to the points, and this has been done by the least squares method (Snedecor 1940, ch. 6). Since the purpose of the work is to calculate intermediate values of L for known intermediate values of S, the required regression equation is that which provides an estimate of L in terms of S, and this is found to be

$$L = 14{\cdot}77 + 32{\cdot}909\ S.$$

This case therefore is one in which the fish- and scale-lengths are not in direct proportion, although their increments are: the type equation may be written $L = A + B{\cdot}S$, whereas with direct proportionality it would be $L = B{\cdot}S$, A and B being constants. However, the intermediate values of L obtained by the use of the device previously mentioned, on the initial assumption of a constant relation between the two dimensions, can be "adjusted" with little trouble. As pointed out by Lee (1920, p. 22), any intermediate fish-length may be calculated, where the above type of relation applies, by means of the formula.

$$L_n = A + \frac{S_n}{S}(L-A)$$

Now, putting L'_n for the intermediate length as calculated by the direct-proportion method, it follows that in this instance

$$L_n = 15 + \frac{L'_n}{L}(L-15)$$

$$= L'_n + 15\ (1-\frac{L'_n}{L}).$$

This formula is similar to those developed for the same purpose by Ramalho (1933, p. 36), Robertson (1936, p. 220), and Lea (1938, p. 19).

There is one obvious objection to estimating intermediate lengths from this single formula. The regression equation which indicated the constant, 15 mm., to be employed in the adjustment, describes a relationship for L and S for all available material, whereas there is theoretically the possibility that it might have been different for material from different year-classes of fish. For example, Walford and Mosher (1943*b*, pp. 13-4) determined this relationship separately for material from four successive year-classes of the North American pilchard, and found that while the position was virtually the same for three of these, it was significantly different in the other case. Other authors (see below) have drawn attention to the same possible source of error. However, in the present case it is not possible to investigate the matter at this stage. As will appear later, there are so many instances of rings missing or very doubtfully

present on the scales that it is impossible to assign a great deal of the material to year-classes at all without the assistance of the information on intermediate lengths, which has therefore to be obtained, for want of any more accurate system, by the use of a single equation derived from the full set of measurements. At a later stage an attempt will be made to see what errors have been introduced through this procedure (section III, 2*c*).

If the L/S relationship in the present case applied over the whole life of the fish, it would follow that the scales were formed when the fish were of average length 15 mm., i.e. equal to the constant A in the equation above, which represents the intercept of the (extrapolated) regression line upon the L axis. However, such is not the case. In an examination of 372 New South Wales pilchards ranging from 25 to 52 mm., it was found that no fish of less than 30 mm. had any scales, all fish of 40 mm. and more had at least some, and that at 32 mm. of length the scaled and scaleless specimens were almost equal in number. Thus the average fish-length at which the scales first appear

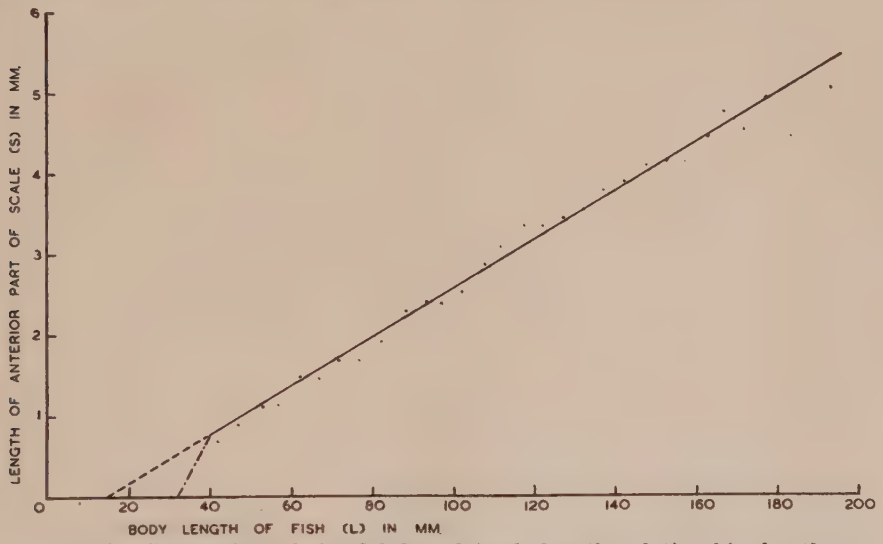

Fig. 4.—Illustration of the fish-length/scale-length relationship for the middle flank scales of the New South Wales pilchard, based on all available data. For further explanation see text.

is probably about 32 mm. This has been indicated in Fig. 4 by a line joining the points $L = 32$, $S = 0$, and $L = 40$, $S = 0{\cdot}75$, although it is likely that the position would be more correctly represented by a curve, and the stray of the last two points at this end of the calculated regression line may indicate this. All this means that after its formation the scale for a short time grows much faster than the fish, after which their length-increments maintain a constant ratio, an implication of this type of relationship which was understood by Van Oosten (1929, p. 340) and subsequent authors. In fact there must be initial acceleration of the growth of the scale after its formation, since the scales always appear late and would never overlap, as they do, if the $L = A + B{\cdot}S$ relationship applied from the moment of their appearance. This was apparently first realized by Taylor (1916, pp. 314-5).

The method by which the relationship has been investigated here for the Australian pilchard, whilst similar to that employed by many other authors, is one that some workers have criticized on various grounds. These objections may be summarized as follows:—

1. Extrapolation of regression systems may lead to quite erroneous conclusions regarding the relation between L and S, especially where the range of observation is limited. This appears to be the essence of the criticisms of Lea (1933). The same point was apparently made by Ottestad (1934, esp. p. 9) and implied by Buchanan-Wollaston (1934, p. 39).

2. The samples of fish from which the L and S data are obtained should be representative of the population for which the relationship is investigated. Thus the mean-points that are plotted will be properly weighted and the question, what is the most likely fish-length for a given scale-length, can be best answered. This was the main point made by Buchanan-Wollaston (loc. cit., esp. pp. 36-7).

3. The material studied should be as homogeneous as possible, and different year-classes should certainly be treated separately. This point was made by Ottestad (loc. cit., pp. 8, 11) and Buchanan-Wollaston (esp. pp. 41, 43), and has been realized also by some other workers.

4. The material of the younger age-groups may not be representative, because the available fish of these groups may (owing to gear selection or other causes) be mostly the larger individuals, a point made by Ottestad (1938, pp. 29-30). This could present a misleading picture of the L/S relationship over the early part of the range if mean-points were calculated in respect of separate age-groups (as some authors have done), but should not have this effect if they are calculated for successive length-intervals. The argument is really a special case of (2).

Now in the present study it can be said that the conclusions that have been drawn are probably unaffected by considerations such as (1) and (4) above, but that they may be affected by those such as (2) and (3). However, it has been explained that it is impossible at this stage to provide for requirement (3) above, and there is also no information which might enable allowance to be made for (2). In spite of these deficiencies it seems obvious that the conclusions drawn from the pilchard material should prove satisfactory for the main purpose with which this part of the study was undertaken: namely, to find a basis for identifying age-rings (by comparison of intermediate lengths in poor scales with those of the clearer ones) and thus for allocating all the scales to the different age-groups of fish. The importance of this will be realized in the following sections.

It will be shown that the range of fish-length over which the first age-rings appear, in the pilchard, falls well within the range for which the L/S relationship has been found to be virtually linear. The same formula:

$$L_n = L'_n + 15\ (1-\frac{L'_n}{L})$$

therefore has been used to calculate all the intermediate fish-lengths. where L'_n is the length as computed by the direct-proportion method.

2. The Data, Their Treatment and Analysis

(a) The Data and Their Treatment

The total number of scales examined was 1,133. This number did not include very damaged or badly regenerated scales, but did include a small number with regenerated centres but readable outer rings. These were obtained from 45 samples of fish taken at various times between April 1939 and November 1941, and including some for every month of the year except March. The samples were procured from a total of 17 general localities over a wide stretch of the New South Wales coast, from Twofold Bay to Tacking Point. They included fish ranging in length from 40 to 193 mm., i.e. over almost the entire range of size at which scales are present.

In tabulating the data, all the material was first grouped according to half-centimetres of fish-length. Within each such group the various samples represented were set out separately in chronological order, and within each sample the scales were distinguished into sets with reference to the different fish-lengths in mm. In some instances scales were recorded in respect of half-centimetres of fish-length, and these were dealt with by taking millimetre-midpoints, e.g. a fish of 15·5 cm. was regarded as 157 mm. long. For each scale there was recorded the scale dimension, and also, as far as they were available, the intermediate fish-lengths L_1. L_2, L_3, etc. and the increments of length T_1, T_2, T_3, etc.

In very many instances the rings were incomplete. Often a ring, or part thereof, could be seen, but was not measurable. Very frequently no definite ring whatever could be perceived, even where all other evidence pointed to the fact that it should have been present.

In several instances, two or three values, instead of one, were entered for L_1, L_2, &c., mostly for L_1. This was due to the presence of one or more "secondary rings"* which are not annual rings although indistinguishable from many of the first and second ones in appearance (see Section III, 1*a*). It was also occasionally due to the partial or complete duplication of a ring, which cases fall into the category of secondary rings. Such duplication could sometimes be easily recognized as a "casquette", i.e. the apical part of a ring of the ordinary type included inside the "spawning-mark" ring of the same year which had obliterated the rest of it (see Section III, 1*a*), and the obvious procedure then was to recognize the "spawning-mark" as the true ring, to bring the records into line with those of the older rings for other scales, which were perforce based almost entirely on the "spawning marks" alone. There was also one scale where the complete ring of the ordinary type was seen inside the "spawning mark" of the same year, which was dealt with similarly. There remained, however, a large number of very difficult cases of duplicated and other secondary rings. To show that such rings are really secondary, and how the distinction between annual and secondary rings is made, warrants some explanation.

*Sometimes called "false rings"; it is shown later that this term is rather misleading.

Firstly a few typical occurrences of secondary rings may be cited. These are:

(1) in a scale from a fish 103 mm., 75,88 are entered for L_1,
(2) in a scale from a fish 147 mm., 79,95 are entered for L_1,
(3) in a scale from a fish 183 mm., 153,162 are entered for L_3.
(4) in a scale from a fish 103 mm., 53,87 are entered for L_1,
(5) in a scale from a fish 96 mm., 57,73,86 are entered for L_1.

Now in each of the first three instances two values are quoted, and the difference ranges from 9 to 16 mm., with a mean at 13 mm.; these cases are representative of many others. Such a figure is obviously too small to be regarded as a likely annual increment of length, especially when the fish is young, and from this it could be concluded that only one of the two represents a true annual ring. However, there is more evidence than this; an examination of the obvious cases in the data as a whole, i.e. those in which there is only one value entered for a ring*, shows that they greatly outnumber those in which there are two values (showing that these cases of double entry are too exceptional for both rings to be regarded as annual), and further, that for each ring the range of single-entry values is fully as great as that covered by paired values. Double entries are usually associated with the first ring, and only rarely with the third and later rings.

Example (4), in which there are two values with a difference of 34 mm., is typical of a small number of cases affecting L_1 only. This difference is certainly of an order much more likely to be an annual increment, though still rather low to occur in early life. However, the number of such cases is very small, and the number of values of the order of the lesser one is much much smaller, even counting single entries (see below), than that of the values of the order of the higher one. This indicates that the lower values cannot be regarded as representing annual rings, because if they were such they would be more numerous than the higher values, since the latter could only occur on scales of fish from a more restricted range of size.

Example (5) represents a rare occurrence, only found in association with the first ring, in which there are three values entered together, two of which are secondary. This instance is a combination of the two types of occurrence already discussed. The first figure represents a secondary ring, and one of the others represents another.

Having demonstrated how occurrences of secondary rings can be recognized as such, it remains to show how, in such cases as the first three and fifth above, the actual distinctions between the secondary and the true annual rings are made. There are five ways in which this can be attempted for this material.

The first method involves a comparison of the rings to determine which is the more complete and/or more distinctly marked, the assumption being that the better ring should be the annual one. This is mostly true but there are frequent exceptions (cf. some cases mentioned below).

*It will be shown later that not all these "obvious" cases of single entry actually refer to true annual rings, but even taking this into account the above conclusions are not invalidated.

The second method is that of comparison with indubitable single-entry values for the same ring for other scales in the same set. For instance, in one set of six scales two have two rings each, with values 84, 101 and 89, 108 respectively entered for L_1; but three other scales in the same set (there was no first ring at all perceptible in the sixth) have indubitable L_1 values of 90, 86, and 88 respectively. This indicates that in the two double entry cases the lower values are more likely to refer to the true first ring than the higher values. Not all cases are as clear as this. The method breaks down with some scales, as is shown later.

The third method, which is an extension of the last and the most useful of all, is that of comparison of the values in question with the modal value for the particular ring under consideration, for all available values for the particular half-cm. size group of fish involved (or for those in the same group in the same sample only, which is better if there is enough material). For example, one scale from a fish of 93 mm. has two rings with values 70, 82 entered for L_1: now if all the values entered for L_1 in the entire 9·0 cm. group are grouped by half-cm. and presented as a length-frequency distribution, there is a mode for the group 8·0 cm., implying that in any doubtful case the true annual L_1 value is most probably the one in, or closest to, the 8·0 cm, range; therefore 82 is here taken as the true value of L_1 and 70 as secondary. The same reasoning was followed in respect of example (4) above.

The fourth method is that of consideration of the time at which the fish was taken. For instance, it will be shown subsequently that the month of the year in which the true first annual ring is most often formed is November; therefore, in any scales taken from yearling fish caught in that month which show two rings, the outer one is, other considerations apart, more likely to be the proper one. This method fails at times.

The fifth method, which is only applicable where there are two or more true annual rings, is that of selection according to the more likely annual increment. For instance, one scale has values 85, 100 entered for L_1, and the indubitable value of L_2 is 131; if 100 is the correct L_1 value, the increment T_2 will be 31, which is quite reasonable, judging from the evidence of other cases; but if 85 is correct T_2 will be 46, which seems much too high. The actual mean values for the various annual increments are worked out later in the paper. This method is very helpful where it can be used.

By the use of all these methods it has been possible, for every multiple entry for L_1, L_2, &c. in the data, to select the value most likely to represent the real annual ring. This work was carefully checked and corrected on a number of occasions and was finally brought to a stage at which it was felt that the results were reliable.

However, some of the single entries may represent secondary instead of true annual rings, on account of the latter being absent. For the same reason, there may be double entries in which both values are secondary (cf. example 5 above). It was therefore necessary to check the data from this aspect.

The methods used here are actually the same in principle as the second, third, and fifth methods just considered. For instance, one scale has the single value 53 entered under L_1, but another in the same set (the only other one for which there is any entry) has the values 53, 84, and of these the former is regarded, following the above methods, as secondary; it seems therefore that the single value 53 in the first scale is secondary also, and only appears as the sole value because for some reason the annual first ring does not appear on that scale. This is obviously a case in which the second method mentioned above, for distinguishing between paired values by comparison with single entries in the same set, would have broken down. In another case, a scale has the double entry 50, 59 for L_1, but as another in the same set (the only other one for which there is any entry), has the values 55, 82, of which the first is secondary, it seems that both the values are secondary in the former scale.

Employing this kind of reasoning and considering every case with care, it is possible to decide that several single-entry values entered for L_1 represent secondary rings. This phenomenon seems occasionally to be associated with the second ring, but not the later rings.

Most other workers studying clupeid scales have likewise failed to find any clear distinction between secondary and at least some of the annual rings from the point of view of general appearance, although one or two claimed to have done so. Tchougounova (1940, pp. 26, 27) recognized certain very slight differences between these " accessory " rings and the yearly ones (i.e. not the spawning marks) for the shad *Caspialosa saposhnikovi,* though granting that their structure is analogous and that the main differences are those of distinctness. Savage (1919, pp. 4-8) was able to distinguish a good many secondary rings in Atlantic herring scales by examining them under polarized light. Most workers seem to have relied for a distinction upon the relative faintness or incompleteness of the secondary rings, and especially upon the alleged circumstance that they do not generally occur upon all scales from the same fish, whereas (it is indicated) they usually do with the " true " rings. This was claimed for the Atlantic herring by Lea (1910) and for the North American pilchard by Walford and Mosher (1943*a*, pp. 8, 9; 1943*b*, p. 4), and even Tchougounova (loc. cit.) appears to have relied at least as much upon such criteria as on differences in actual ring structure. Several other authors have worked in the same way for clupeid and other fish scales. These criteria do not cope very well with the position as it is encountered in the present pilchard material, where there may be secondary rings as distinct or complete as the annual ones or more so, or present where the annual rings are suppressed, and, although admittedly there is only a limited number of sets of several scales from the same fish*, it does not appear from these that secondary rings are generally confined to one or two scales only. Perhaps this material is by any standard less easy to interpret than that on which other authors have worked, but it may be noted that some other writers have stated, for the Atlantic herring for example, that they consider that the difficulties of distinguishing " false " or secondary rings have been unduly minimized by such workers as Lea.

* About 40 per cent. of the total number of scale sets, but some of these were from very young fish which bore no rings.

Among those who were of this opinion were Schneider (1910)*, Paget (1920, p. 21) and Johansen (1924, p. 23), who claimed to have encountered on herring scales precisely such difficulties of interpretation as have been noted by the present writer. Lea (1919, p. 99) also says for the herring: "I was at first of the opinion that the position of all kinds of these 'secondary rings' varied from scale to scale, and that their disturbing influence might therefore be eliminated by examining a sufficiently large number of scales from each fish. Objections to this have, however, been raised by Hellevaara . . . . , who considers that secondary rings may be found, the position of which corresponds on the different scales of a fish—being, however, in some scales almost indistinguishable." Actually, in view of the almost universally accepted proposition that the rings on a scale are a sort of register of certain events in the life of the fish, it would be highly illogical to expect that certain of these, the secondary rings, would not appear on many if not all of the scales from at least the same part of the same fish. One can imagine without much difficulty that there might well be important differences between the scales of the same fish as regards the distinctness of *both* secondary and true rings, which certainly do occur. However, it is extremely difficult to suppose that a ring of a certain category will fail absolutely to appear in more than a very small minority of scales from the same fish, while others will be visible on all of them, as some workers have claimed; and, as far as can be seen from the present work, at least in such cases secondary rings are no less liable to occur from scale to scale than true annual ones, although the distinctness of either may certainly vary greatly as stated above, and sometimes both seem to fail altogether. The secondary or accessory or false rings are not adventitious marks, but have their origin in certain happenings in the life of the fish just as do the other rings, and will therefore tend to occur, as they do, on at least a large proportion of its scales. The real reason that scale-readers seek to distinguish and disregard these rings for age-study purposes is not that they do not represent events in the life of the fish, but that they do not represent those major events which, while not necessarily precisely annual (see next section) are sufficiently nearly so, and sufficiently general in their influence, as to be of use for age study. One might also say that the secondary rings associated with say the first annual ring, do occur, in sum, much less commonly than that "true" mark does; but not because they are found only on the minority of scales from each fish, but because they are found only on the scales of a minority of the fish themselves, owing to the fact that they certify events which are not of such general occurrence in the population as to leave their imprint on a relatively large number of individuals. It follows from all this that the term "false rings" as applied to these marks is misleading.

However, most scale-readers do seem to have been able to distinguish secondary rings in practice, for the herring at least, since the results of the age-studies made by them seem to be quite valid from other evidence. This rather suggests to the writer that even those authors who have apparently minimized these difficulties in their writings have employed stricter criteria in the actual scale-reading work done.

* Not available to the writer; quoted in Graham (1929*a*) and elsewhere.

Some workers with other clupeids agree with what has been shown here as to the special tendency for secondary rings to be associated with the first annual ring. Fage (1913, p. 323) observed this for the European pilchard, and Tchougounova (1940, p. 28) for the Caspian shad. Savage (1919, p. 5) also noted for the herring that where two rings occur close together it is the inner one which is secondary. This is generally so with the pilchard too.

The problem of the treatment of the data does not even end here. Owing to the fact that there are a great many scales in which some rings are obviously missing, often one cannot feel certain that the number of rings noted is not too low. One is frequently in doubt as to whether to allot a particular value to L_2 or L_3, for example. It is, however, possible to allot all the values for annual rings with certainty in the majority of scales and with probable correctness in most others, thus providing a basis for correct deductions as to age. The procedure adopted has been to make the allocations by consideration of obvious cases, of modal values for the group, and of the time of capture of the fish in conjunction with the season of formation of the ring. The latter question is next discussed.

(*b*) *The Times of the Year at Which the Rings are Formed*

An attempt has been made to distinguish those scales in which annual rings appear close enough to the scale-edges to indicate that at the time of collection they had been formed fairly recently. The months for which these scales constitute the highest proportion of the total material will then represent the periods at which the rings are usually formed.

There were clear indications in the data that the first annual ring is formed at a different season from the later ones, which are formed at about the same time of year. It was therefore necessary to investigate the first one separately, as well as possible at the present stage of the study. For consideration of this first ring there were taken into account all scales in the 6·5 to 11·0 cm. fish-length groups inclusive, and for the others all the rest of the material. This was because the 6·5 cm. group is the first one in which any scale is found to bear a proper annual ring, whereas in the 11·5 cm. group there are the first clear cases of two-ringed scales. It will be found that this grouping still includes some two-year fish, but this was not obvious at first sight. It was at first decided to accept, as L_n values presumably representing recently formed rings, any which were no more than 5 mm. below the size of the fish from which the scales came, but it was found that on this basis the data for the first ring would be rather inadequate for the present purpose. Therefore, within the first range of material mentioned above, rings with values up to 10 mm. below fish-size were accepted. This results from the fact, already established from the studies with the Petersen method, that the fish are very fast-growing at this stage and so the margin of the scale is very quickly added to; it can be shown that the conclusions are unaffected. For the rest of the material the 5 mm. limit was adhered to, though even this meant that the width of the margin outside the ring was still a somewhat variable proportion of the increment of the succeeding year (cf. Section III, 2*d*, where mean increment values are established). However this could not be avoided at this stage, because of uncertainty as to what even the mean increment values were and which rings were which in respect of age, in some cases, owing to omitted or doubtful rings as explained before. It seems impossible that any of these approximations could have importantly affected the conclusions reached here.

It is clear that for the great majority of scales the first annual ring is formed between October and December, November being the principal month. For a few others it might appear that it is formed between May and July, but it will be clear from what follows in this and the next section of the study that in these cases the ring is the second and not the first, the discrepancy having arisen from the roughness of the grouping of the scale material in this part. It may be added that the L_n values entered for these few rings were all of 110 mm. or over, i.e. higher than any entered for the other rings whose scales are included in the third column above.

Tabulating the data for the first range of fish-lengths mentioned above:

Month	Total No. of Scales	No. of Scales with Rings in 10 mm. Limits	Per cent.
September	63	1	1·6
October	91	12	13·2
November	94	19	20·2
December	116	17	14·7
January	6	—	—
. . . .	...	..	....
April	1	—	—
May	7	1	14·3
June	5	—	—
July	6	5	83·3

For the second range of material, i.e. from fish of length 11·5 to 19·0 cm., the position is set out in the next table. From what was said above this should reveal the season of formation of the second and subsequent rings; i.e. the second to the fifth inclusive, since there was no ring that could be regarded as a sixth or later one (see next section). It was obvious from a superficial examination of the data that the general season of formation was the same for all these rings, except possibly the fifth.

Month	Total No. of Scales	No. of Scales with Rings in 5 mm. Limits	Per cent.
April	119	8	6·7
May	72	6	8·3
June	133	32	24·1
July	118	38	32·2
August	33	13	39·4
. . . .	...	..	....
October	54	16	29·6
November	18	—	—
. . . .	...	..	....
January	22	—	—

This shows that the rings after the first are liable to be formed from April to October, or possibly even a little earlier (for want of evidence for March), but mainly between June and October. A shade of doubt attaches to the fifth ring in this connection because the only data are for October, in respect of which the observed rings are within the 5 mm. limits. However, there is no

reason to suppose that the general season is actually different from that for the other rings, especially as October is quite an important month for their formation also (see Section III, 3).

Obviously then, the first ring is formed at quite a different season from the second and subsequent ones. Since the fish are spawned in the general winter season the latter marks are thus real annual and anniversary rings, while the first one is neither, being formed in the spring and summer following the first anniversary of birth, when the fish are on average about $1\frac{1}{4}$ years of age. There is more discussion of this point later, but meantime the first ring can be spoken of for convenience as the first annual ring, since there is no sign of any other mark on the scales which could have that significance.

It might be suggested that the "secondary rings" represent this first anniversary ring in the scales in which they appear, since most of them are associated with the first ring and are formed before it, as noticed in the last section. To test this the time of formation of these early rings was investigated on the same lines as above. The data are too scanty to be worth presentation, but as far as they go the results indicate that the secondary mark that often precedes the first annual ring is mostly formed about September or early October, i.e. not long before the first ring itself. Some of them may actually be formed in the winter, i.e. at the first anniversary of birth, but these, if any, would be very few. There is also one case of a secondary ring on a scale from a fish 52 mm. long, taken in December, and apparently (evidence of Petersen method, see Fig. 2) only a few months old.

(*c*) *Age-for-size*

The last phase of the treatment of the data is the allocation of L_n values to the appropriate rings in doubtful cases, and the formulation of definite conclusions as to the age of fish at various sizes. Because the nature of the data made this task still rather difficult, it seems desirable to describe briefly the situation that was encountered in respect of the material of each half-cm. fish-length group.

The scales in the 4·0 *cm. group* were all obtained from fish taken in the spring and early summer and bear no rings at all. From consideration of the length frequencies in the samples the spring-summer in question is always clearly the first of life, and these fish are thus only a few months old.

In the 4·5 *cm. group* most of the material is of the same character, but one sample belongs to the second spring of life, and there is also one from the winter which must be intermediate in age between the other groups. There are no rings on any of the scales. The fish in the second spring of life can be reckoned as approximately $1\frac{1}{4}$ years old on average. This reasoning is merely an application of the Petersen method, but is included here for completeness.

In the 5·0 *cm. group* there are scales from samples in the first summer, the the first autumn, and the second spring of life, which are respectively a few months old, just under a year old, and about $1\frac{1}{4}$ years old. The only one to bear a ring (secondary) is one of those in the first summer of life.

From this stage onwards there is no further material that can be regarded as belonging to the first spring and summer of life. In the 5·5 *cm. group* there are scales from the first autumn (Plate 1, Fig. 1) and the second spring, and one of the latter bears a secondary ring. In the 6·0 *cm. group* there are scales from the second spring only, with (secondary) rings in one or two cases. In the 6·5 *cm. group* there is again some material from both this period and the autumn preceding, and of the former scales one or two bear secondary rings and one bears an annual one. Since this last has $L_1 = 64$ it appears that such rings can occasionally be formed in fish in the 6·0 cm. range. In the 7·0 *cm. group,* however, there seem to be no instances of annual rings on the scales, which are all from fish caught in the second spring and summer. It is probable that more intensive sampling would reveal these, since there are a few instances of older scales in the rest of the collections which bear proper first rings with L_1 values running from 66 upwards, including some in the range 70–74.

The first annual ring becomes really noticeable in scales from the 7·5 *cm. group* of fish. All scales here refer to the second spring of life, and several bear rings, some secondary and some annual.

In the 8·0, 8·5, 9·0, and 9·5 *cm. groups* the scales again all come from fish in the second spring and summer of life and bear true first rings in many instances (Plate 1, Fig. 2).

A somewhat different situation obtains in the 10·0 *cm. group.* Again most of the scales are from fish taken in what is obviously their second spring and summer, and there is thus no doubt that the single annual ring that many of them bear represents their age quite well (Plate 2, Fig. 2). However, there is also a sample of scales from a fish taken in the winter, but with one ring only, which is undoubtedly the first annual one; whereas, since the winter in question is obviously the second one after hatching, and since the second ring is formed between the autumn and spring, there might be expected to be two rings on these scales. Apparently either the period for the formation of the second ring in these particular scales has not been quite reached, or else for some reason the appearance of this ring has been inhibited, as often seems to happen in other scales. Thus the 10·0 *cm. group* apparently consists mainly of fish which average rather less than 1½ years old (I-group), but to a slight extent also of fish about two years old (II-group).

One might expect to find these two groups of scales also represented in the 10·5 *cm. group,* or else the II-group only, but actually in this material this is not so, all the scales being from fish in their first spring and summer, with one true ring only (Plate 3, Fig. 1). This must be due to incomplete sampling, since in scales from older fish there are rings with L_2 values falling in this size-range, and so the conclusion is that 10·5 cm. fish may include both I- and II-group individuals.

In the 11·0 *cm. group* there are still some spring fish of the I-group, but there is also a significant body of material (about half the total) taken in what is obviously the second autumn and winter of life, i.e. II-group fish, which might be expected to show two annual rings. However, there are actually

no obvious cases of these, and there is thus the problem of allocation of intermediate length values to particular rings. The value in the autumn-winter scales of this group fall roughly into two groups, and since these will obviously correspond to L_1 and L_2 respectively the allocation is not particularly difficult. This shows that several of the scales should actually be two-ringed, since the ring they bear is clearly the second, but that for some reason the first does not appear. On the other hand some of these II-group scales only bear a first ring, and so either the second ring has not yet been formed, or else it does not appear at all. Finally there are scales in which neither ring is to be seen. These difficulties recur in all the subsequent material, and have made the whole study most difficult.

In the 11·5 *cm., group* there are only autumn-winter fish, which may all be expected to be two years old. This is quite obvious where two annual rings appear on the scales, but other cases are less simple. With a frequency distribution of the values in the whole group as a guide, and considering the range of values of L_1 and L_2 in obvious cases, this is achieved as before. The results indicate a position as to age essentially the same as for the autumn-winter fish in the last group, all fish being two years old for practical purposes, some perhaps just under it (Plate 2, Fig. 1).

The 12·0 *and* 12·5 *cm. groups* can be analysed in the same way, and consist of the same elements in respect of season and age (Plate 4, Fig. 1; Plate 5). However, apparently some three-year-old fish may occur in the 12·5 cm. range, since there is one instance of a scale from an older fish which has $L_3 = 129$.

The data of the 13·0 *and* 13·5 *cm. groups,* however, present some greater difficulties in analysis. The scales are all from fish of autumn, winter, and spring, i.e. a time corresponding to the spawning season, and one might at first suppose that all these fish are also two years old or a little more or less. Some scales are definitely from such fish (Plate 3, Fig, 2; Plate 4, Fig. 2), but others are obviously from three-year old fish, though none show three clear rings on the same scale (one has two quite clear and the third present, but unmeasurable). The length frequency distributions of all the L_n values for these scales show that there are four modal points, at approximately 8·5, 10·0, 11·5, and 13·0 cm. respectively, and from a consideration of this and all the other information available it appears that these scales are a mixture of material from II- and III-group fish. Since the third ring is formed at the same season as the second this is quite reasonable. Most III-group individuals seem to have scales with values of L_1, L_2, and L_3 of approximately 8·5, 11·5, and 13·0 cm. respectively, but the II-group fish usually have L_1 and L_2 at approximately 10·0 and 13·0 cm. The sorting out of the L_n values to their proper rings is an extremely difficult process for the individual scales even with this much guidance, since most of them lack at least some of the rings which it is clear they should have, and depends largely upon a consideration of the most probable annual increments. It reveals that in the 13·0 *cm. group* the II– and III–group fish scales constitute respectively 55 and 45 per cent. of the total, and in the 13·5 *cm. group* 39 and 61 per cent., which are reasonable proportions.

In the 14·0 *cm. group* there is the first indubitable case of a three-ringed scale, with values 95, 121, and 141 mm. for L_1, L_2, and L_3; and it is clear, from applying the methods mentioned above, that all the scales available are referable to III-group fish, even though most of them lack some at least of their rings. The material was collected between the autumn and spring and thus all the fish in question would have been about three years of age. However, a few fish may occur at this size which are only two-year individuals, since there are two scales from still older fish which have indubitable L_2 values of 140 and 143.

Much the same applies to the 14·5 *cm. group* except that there is no evidence whatever that any fish at this size are less (or more) than about three years old in the autumn and winter, when all the material was collected (Plate 6, Fig. 2). There are several obvious cases with the full complement of three rings.

In the 15·0 *cm. group* there is again a mixture of scale material. A good number of scales from fish taken between the autumn and spring are to be reckoned as from three-year-old fish, from a consideration of obvious cases of three-ringed scales and comparison with these, and other evidence of the kind discussed above. There is also a group of scales obtained in January, many of which bear three indubitable rings and the rest of which resemble them very closely as far as the available L_n values are concerned; these are clearly from fish about three and a half years of age, and the third ring is always well inside the scale margin. Finally there are some scales taken in the autumn which have only three rings at most, but with the third even further inside the margin, and it appears that these are from pilchards just approaching their fourth anniversary of birth, although the fourth ring has not been formed. Hence, the fish in this range of size are to be regarded as partly of the III- and partly of the IV–group, the proportions in this material (omitting the intermediate January scales) being about 77 and 23 per cent. respectively.

In the 15·5 *cm. group* the position is essentially the same, there being scales taken between the autumn and spring which are in part referable to the III-group (74 per cent.) and in part (26 per cent.) to the IV-group, and some of the latter have four indubitable rings. Then there is also some material in respect of January which is apparently intermediate in age. Similarly in the 16·0 *cm. group* there are scales obtained between the autumn and spring some of which are to be placed in the III-group (56 per cent.) and some in the IV-group (44 per cent.), with many definite cases of both (Plate 6, Fig. 1). The gradual change in the percentages of the two age-groups with increasing fish-sizes is in the expected direction.

For the 16·5 *cm. group* all the scales were taken in the winter and spring, and even where the scales do not bear four rings there is sufficient evidence, from comparison of L_n values with those in these indubitable cases, to show that they are all referable to the IV-group (Plate 7, Fig. 1). However, there must be some slight admixture of III-group fish at this size, because one scale from a larger fish has $L_3 = 165$.

For the 17·0, 17·5, *and* 18·0 *cm. groups,* the available material is again all from the winter and spring, and while not all scales have four rings it is clear that they all belong to the IV-group of fish (Plate 7, Fig. 2). There is no suggestion of fish at any lower or higher age, although the material is not very abundant.

There are no scales available from fish in the 18·5 cm. class interval, but there are some from one fish in the 19·0 *cm. group,* which bear five rings (Plate 8, Fig. 1). This specimen was taken in October, and thus had not long turned five years. There are no scales in respect of any larger fish.

Summarizing:

1. The 0-group fish (mostly but a few months old) are all those at 4·0 cm. or less, and some of those up to and including 5·0 cm.

2. The I-group (mostly somewhat over one year, at least over 6·5 cm.) are some of those at 4·5 and 5·0 cm., all at higher sizes up to 9·5 cm., and some up to 11·0 cm.

3. The II-group (two years) are some of those from 10·0 to 11·0, all at 11·5 and 12·0, and some up to 14·0 cm.

4. The III-group (three years or rather more) are some of those from 12·5 to 14·0, all at 14·5, and some up to 16·5 cm.

5. The IV-group (four years) are some of those from 15·0 to 16·5 cm., possibly all at 17·0 to 18·0 cm., and perhaps some larger ones.*

6. The V-group includes at least some fish at 19·0 cm. and possibly at lesser or greater sizes.*

These findings agree very well with those from the Petersen method as far as the first three groups are concerned. The data on the III-group were very meagre in respect of the Petersen method, but they do not conflict with anything shown here. There is a slight discrepancy between the two sets of results as far as the IV-group is concerned, which can probably be attributed to the scarcity of material on both counts.*

In view of the rather limited material and the fact that the scales read were generally selected from groupings of those from several fish of the same size, one must admit the possibility of an even greater overlapping of age-groups, by size of fish, than the above analysis reveals. That is to say, some of the half-cm. groups listed above as unmixed in respect of age might be found to contain a portion of other age-groups in a larger material. From all indications, however, these proportions would not be large.

It is now possible to see whether there are differences of practical significance in the L/S regression (see Section III, 1*d*) from material of different year-classes. To the extent that they are available, the paired measurements of L and S were averaged as before for successive half-centimetre intervals

* Some more scales have been read since the above was written, and a few fish at lengths down to 165 mm. have been identified as belonging to the V-group. Thus there is a considerable overlapping of the IV- and V-groups in respect of fish-lengths. Furthermore, the age of one fish 187 mm. long has been determined as six years.

of L, and regression lines fitted for the data of each year-class separately. The data are set out in Table 4, and Fig. 5 depicts the regression lines for the different classes as compared with that derived before for all the data combined. The equation in this former case was

$$L = 14{\cdot}77 + 32{\cdot}909\ S.$$

Those for the separate year-classes are as follows:

$$1940.\ L = 21{\cdot}97 + 25{\cdot}977\ S.$$
$$1939.\ L = 24{\cdot}30 + 29{\cdot}302\ S.$$
$$1938.\ L = 11{\cdot}93 + 32{\cdot}551\ S.$$
$$1937.\ L = 7{\cdot}13 + 33{\cdot}863\ S.$$
$$1936.\ L = -21{\cdot}59 + 41{\cdot}431\ S.$$

That for the 1935 class was not calculated, since there are only three points and they lie practically on a straight line.

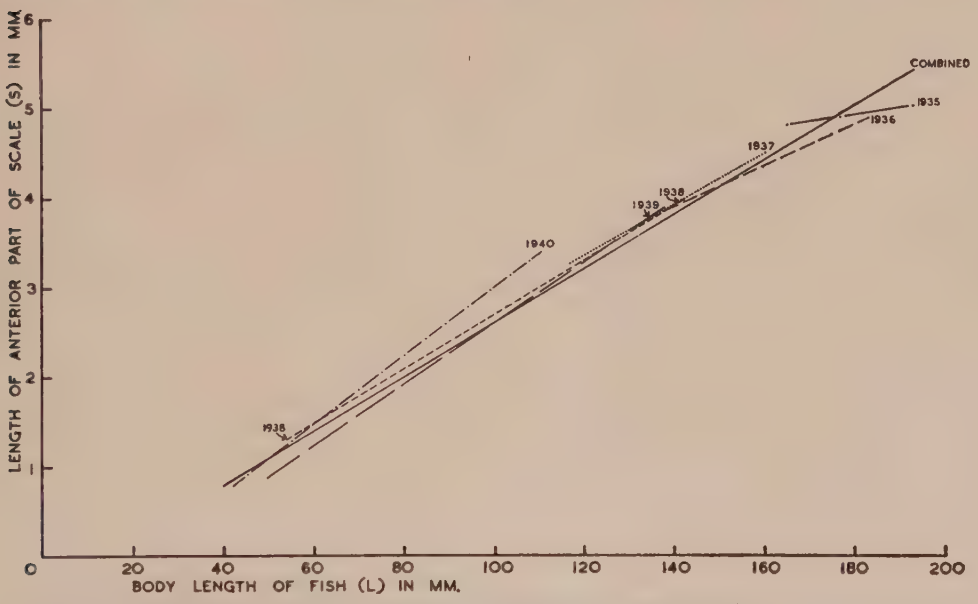

Fig. 5.—Illustration of the fish-length/scale-length relationship for the middle flank scales of the New South Wales pilchard, shown for all available data combined (cf. Fig. 4) and for the data of each year-class separately. For further explanation see text.

It can be seen that the comparison is very reasonable over the range of L and S for which information was available in respect of the different year-classes. If the lines were extrapolated beyond the ranges, there would be some serious discrepancies in respect of the 1935, 1940, and 1936 information at least; but this is of course not permissible, and there can be no doubt that, if data had been available in reasonable quantity for extended ranges of L and S, the agreement would have been very much better. As it is, it can be shown that the intermediate lengths calculated on the basis of the original overall formula could not have been inaccurate from this standpoint to any greater extent than one or two mm. in any case whatever, even allowing that all the various

regression lines depict the position correctly for the particular year-classes in question, which it is practically certain that at least some of them do not. For the overwhelming majority of cases no alteration whatever would have been involved.

TABLE 3

MEANS OF SCALE-LENGTHS (S) AND OF CORRESPONDING FISH-LENGTHS (L), FOR SUCCESSIVE HALF-CENTIMETRE INTERVALS OF L, FOR ALL AVAILABLE MATERIAL

Length-group (cm.)	Mean Fish-length, L (mm.)	Mean Scale-length, S (mm.)	Number of Observations
4·0	41·90	0·684	20
4·5	47·14	0·905	35
5·0	52·68	1·113	37
5·5	56·95	1·161	38
6·0	61·73	1·483	45
6·5	66·79	1·473	42
7·0	71·09	1·722	53
7·5	76·58	1·683	33
8·0	82·00	1·929	28
8·5	87·93	2·297	27
9·0	92·35	2·412	43
9·5	97·07	2·383	27
10·0	101·84	2·516	50
10·5	107·66	2·888	35
11·0	111·80	3·090	20
11·5	117·57	3·343	21
12·0	122·06	3·362	72
12·5	127·08	3·442	64
13·0	131·74	3·546	43
13·5	137·07	3·806	42
14·0	141·73	3·919	22
14·5	147·29	4·111	17
15·0	152·50	4·160	28
15·5	156·94	4·130	34
16·0	161·25	4·448	16
16·5	166·41	4·775	17
17·0	171·33	4·543	18
17·5	177·00	4·915	4
18·0	183·00	4·442	6
18·5	..	..	..
19·0	193·00	5·058	5
			Total 942

The original overall equation was computed from a total of 942 pairs of observations on L and S (see Table 3), whereas the total number of pairs utilized in establishing these separate equations was 810. That is to say, there were 132 scales, 14 per cent. of the total, which could not be allocated to year-classes, i.e. whose age could not be told at all. Since this suggests a relatively high degree of efficiency in scale-reading, considering the extreme difficulties, it is only proper to say that this was not so. As the preceding part of this section will have shown, for the scales of the smaller fish the allocation was largely made, or could have been made, on the basis of an application of the Petersen method alone. The scale-work did not become a critical factor in age-determination until sizes of fish were reached at which the I- and II-groups overlapped, i.e. 10·0 cm. and upwards. If the totals of scales from these fish are compared in Tables 3 and 4, it is found that out

TABLE 4

MEANS OF SCALE-LENGTHS (S) AND OF CORRESPONDING FISH-LENGTHS (L), FOR SUCCESSIVE HALF-CENTIMETRE INTERVALS OF L, FOR MATERIAL OF EACH YEAR-CLASS SEPARATELY

Length-group (Cm.)	1940 Class			1939 Class			1938 Class			1937 Class			1936 Class			1935 Class		
	L (mm.)	S (mm.)	Number Observations	L (mm.)	S (mm.)	Number Observations	L (mm.)	S (mm.)	Number Observations	L (mm.)	S (mm.)	Number Observations	L (mm.)	S (mm.)	Number Observations	L (mm.)	S (mm.)	Number Observations
4·0	41·90	0·684	20	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
4·5	46·25	0·954	28	49·00	0·853	7	..	..	..	..	..	..	..	..	..	..	..	..
5·0	52·15	1·141	20	52·91	0·947	11	54·00	1·325	6	..	..	..	..	..	..	..	..	..
5·5	..	..	..	56·86	1·141	35	58·00	1·403	3	..	..	..	..	..	..	..	..	..
6·0	..	..	..	61·73	1·483	45	..	..	..	..	..	..	..	..	..	..	..	..
6·5	..	..	..	66·83	1·478	41	65·00	1·250	1	..	..	..	..	..	..	..	..	..
7·0	..	..	..	71·09	1·722	53	..	..	..	..	..	..	..	..	..	..	..	..
7·5	..	..	..	76·58	1·683	33	..	..	..	..	..	..	..	..	..	..	..	..
8·0	..	..	..	82·00	1·929	28	..	..	..	..	..	..	..	..	..	..	..	..
8·5	..	..	..	87·62	2·192	21	89·00	2·665	6	..	..	..	..	..	..	..	..	..
9·0	..	..	..	92·24	2·343	37	93·00	2·838	6	..	..	..	..	..	..	..	..	..
9·5	..	..	..	97·07	2·383	27	..	..	..	..	..	..	..	..	..	..	..	..
10·0	..	..	..	102·00	2·490	46	100·00	2·820	4	..	..	..	..	..	..	..	..	..
10·5	106·00	3·104	12	106·96	2·775	23	..	..	..	..	..	..	..	..	..	..	..	..
11·0	110·00	3·495	2	110·00	2·742	6	113·00	3·197	12	..	..	..	..	..	..	..	..	..
11·5	..	..	..	..	..	..	117·80	3·237	15	117·00	3·607	6	..	..	..	..	..	..
12·0	..	..	..	..	..	..	121·95	3·343	62	122·40	3·496	10	..	..	..	..	..	..
12·5	..	..	..	..	..	..	127·50	3·386	20	127·00	3·630	3	..	..	..	..	..	..
13·0	..	..	..	..	..	..	133·50	3·515	4	131·43	3·607	7	..	..	..	..	..	..
13·5	..	..	..	138·00	4·180	2	137·67	3·997	6	135·83	3·825	6	138·00	4·030	4	..	..	..
14·0	..	..	..	..	..	..	142·00	3·993	3	141·50	3·840	2	142·00	3·913	3	..	..	..
14·5	..	..	..	..	..	..	..	..	..	146·36	4·004	11	149·00	4·308	6	..	..	..
15·0	..	..	..	..	..	..	..	..	..	151·71	3·990	7	152·00	4·359	16	..	..	..
15·5	..	..	..	..	..	..	..	..	..	157·30	4·154	10	157·54	4·414	11	..	..	..
16·0	..	..	..	..	..	..	..	..	..	160·00	4·794	5	162·00	4·234	10	..	..	..
16·5	..	..	..	..	..	..	..	..	..	..	..	..	167·00	4·809	10	165·00	4·820	5
17·0	..	..	..	..	..	..	..	..	..	..	..	..	171·33	4·554	18	..	..	..
17·5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	177·00	4·915	4
18·0	..	..	..	..	..	..	..	..	..	..	..	..	183·00	4·450	4	..	..	..
18·5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
19·0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	193·00	5·058	5
..	..	..	82	..	..	415	..	..	148	..	..	69	..	..	82	..	..	14

of 514 only 384 could be assigned to different ages, i.e. 75 per cent. instead of 86 per cent. as suggested above*. Even this degree of efficiency is probably fairly satisfactory in view of the incomplete and difficult character of much of the evidence from rings, although this work was greatly assisted by comparisons from scale to scale in the same set and sample and group, and it is certain that results as good could not be obtained with say a small number of isolated scales from fish of a great variety of sizes, or from fish of unknown size. Probably almost any fish could be assigned to its correct age if there were at least three or four scales made available from it, which was not done in the majority of cases in the present study, and is in many cases impossible because of loss of scales.

(d) Mean Size-for-age, and Variation Thereof

It is now desirable to establish the mean lengths attained by the New South Wales pilchard in successive years of life. This work is based upon an analysis of intermediate length values, which show the sizes attained at the formation of the successive annual rings. However, it is not permissible to regard, say, the mean of all available values of L_1 as being necessarily the average length at the formation of the first ring, because there is considerable variation in respect of such data, which could arise from a number of possible causes.

Buchanan-Wollaston (1931, p. 52) spoke of factors causing differences and inducing similarity between the growth of individuals as "divergent" and "convergent" respectively. Kesteven (1942, pp. 42-7; and 1946, pp. 43-6) proposed instead the terms "dispersive" and "adducent". As possible dispersive factors in general cases he listed the following types of effects:

1. Sex.
2. Locality.
3. Brood (referring to the possibility of different styles of growth for various year-classes).
4. Lee's Phenomenon (referring to differences in intermediate lengths for various age-groups).
5. Genetic.

The only adducent factor is the effect of:

6. Growth compensation.

Unfortunately no proper investigation of the possibility of growth difference between the sexes can be made in this case. As explained before, the majority of the scales cannot be identified as to the sex of the fish from which they came. However, it is most unlikely that there is any substantial variation on this score, firstly because this is the definite impression received from an appraisal of the data that are available for fish of known sex, and secondly because such

* Actually the total number of scales at these sizes read for age was higher than this, for it will be recalled that nearly 200 scales were omitted from all the computations of the L/S relationship because the corresponding fish-lengths were only available in half-cm.

TABLE 5

MEANS OF CALCULATED INTERMEDIATE LENGTHS (L_1, L_2, ETC.) BY AGE-GROUPS, WITH MEAN FISH-LENGTHS (L) IN RESPECT OF CORRESPONDING SCALES, ALL YEAR-CLASSES COMBINED, NORTH AND SOUTH COASTS (IN MM.)

—	Age-group	L_1			L_2			L_3			L_4			Total for Group	
		No.	Mean L_1	Mean L	No.	Mean L_2	Mean L	No.	Mean L_3	Mean L	No.	Mean L_4	Mean L	No.	Mean L
North Coast ..	I	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	II	51	94·14	124·31	75	117·37	122·43	..	..	..	..	..	..	104	123·15
	III	24	90·54	157·75	75	118·85	147·46	59	143·61	150·36	..	..	..	102	148·37
	IV	14	96·14	163·71	30	124·83	163·23	44	146·32	165·02	31	161·32	167·16	49	165·02
South Coast ..	I	101	86·80	97·69	..	..	..	..	..	..	..	..	..	101	97·69
	II	13	96·75	129·08	11	121·18	129·55	..	..	..	..	..	..	17	127·88
	III	7	96·29	158·29	6	116·00	155·17	19	144·68	155·42	..	..	..	21	155·76
	IV	6	89·00	169·17	6	122·33	170·33	10	151·50	174·70	24	165·50	171·21	26	171·77

growth-rate differences between sexes are apparently not very important in clupeids generally.* Also, the mean lengths of males and females were alike in many samples that appeared to consist mainly of fish of the same age.

Leaving this aside, the data on intermediate lengths might be set out as in Table 5. This attempts to identify possible locality effects as between the north and south coasts of New South Wales, the south coast being defined as extending up to and including Port Jackson and its neighbourhood, while the north coast covers all waters further north. For each of these areas the means of available counts of L_1, L_2, &c., are shown for each age-group separately (I, II, &c.) where available, but without distinction as to year-classes. There has also been shown, the mean of the corresponding fish-lengths (L) for the scales in question, for each intermediate length separately and for the total of scales in each age-group from which any intermediate lengths were available. This is then a preliminary attempt at an analysis of the possible dispersive factors in connection with locality and age-group, while ignoring that possible factor associated with year-class (brood). It is seen firstly that any effective comparison whatever between the two localities must be very difficult, because whereas all the material in respect of the I-group refers to the south coast, the great bulk of that in respect of the later groups refers to the north coast; this was because the older fish were scarce in the former region at the time the bulk of the collections were made, while no great amount of work was ever done on the north coast at the time of year when the younger pilchards would be available. Even so, judging from the data as they stand, any such variations associated with locality must be rather unimportant. Secondly, there is no clear evidence of Lee's phenomenon (diminishing values for intermediate lengths in respect of increasing age) or of any other consistent trend associated with the different age-groups.

However, there is one dispersive factor in this material that was quite conspicuous during the actual scale-reading process, and that is one not included in the above list, the effect associated with the sizes of the fish. Since it appears from Table 5 that there is some slight variation in the means of fish-length (L) corresponding with the means of the different intermediate lengths for each age-group (e.g. a range of over 10 mm. in respect of the III-group for the north coast) it is desirable to investigate this source of variation further. It will be shown that the effects of this factor do not substantially alter the position as revealed in Table 5, but the matter is of considerable interest in connection with the general academic study of growth-rate.

In Table 6 there are set out the means of L_1, L_2, &c. for the separate age-groups, and of the fish-lengths (L) for the corresponding scales, for successive half-cm. intervals of L, for all north coast material without distinction as to year-class. To eliminate that variation in L which would result from different times of measuring in the biological year, the data relate (as also in Table 5) only to material collected in the seasons at which the rings are

* Graham (1929*a*, p. 16) quotes Lee (1912, unavailable to the writer) as noting such differences, but apparently not large ones, in respect of the Atlantic herring; W. F. Thompson (1916, p. 65) found for the Pacific herring that females grew very slightly faster than males, and the same seems to be true of the European pilchard (see De Buen, 1935, pp. 98-102).

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TABLE 6

MEANS OF CALCULATED INTERMEDIATE LENGTHS (L_1, L_2, ETC.), AND OF FISH-LENGTHS (L) FOR CORRESPONDING SCALES, FOR SUCCESSIVE HALF-CENTIMETRE INTERVALS OF L IN EACH AGE-GROUP (II–IV) SEPARATELY, ALL YEAR-CLASSES COMBINED (IN MM.), NORTH COAST ONLY

(Numbers of observations omitted to save space; means based on less than 5 are shown)*

Length-group (cm.)	II.				III.						IV.							
	L_1	L	L_2	L	L_1	L	L_2	L	L_3	L	L_1	L	L_2	L	L_3	L	L_4	L
11·0	97·50*	112·00	110·83	113·67	..	..	..	..	..	..	..	..	..	..	..	..	..	..
11·5	88·46	117·08	111·79	117·63	..	..	..	..	..	..	..	..	..	..	..	..	..	..
12·0	91·38	122·46	117·000	121·71	..	..	..	..	..	..	..	..	..	..	..	..	..	..
12·5	94·92	127·43	121·05	127·24	..	..	..	..	..	..	..	..	..	..	..	..	..	..
13·0	104·20	132·60	127·17	132·67	86·50	131·40	112·88	131·62	..	..	..	..	..	..	..	..	..	..
13·5	106·20	137·00	131·00*	137·00	91·67*	136·00	114·25	136·75	131·57	136·57	..	..	..	..	..	..	..	..
14·0	..	..	..	..	94·50*	142·00	112·00	141·80	138·43	142·14	..	..	..	..	..	..	..	..
14·5	..	..	..	..	85·57	147·00	116·54	147·46	139·84	147·63	..	..	..	..	..	..	..	..
15·0	..	..	..	..	..	..	127·00*	151·50	144·00	151·67	89·00*	152·00	119·25*	153·50	135·00*	153·33	..	..
15·5	..	..	..	..	95·60	156·80	124·88	156·75	149·43	157·00	92·00*	157·00	123·80	157·00	146·50	157·00	152·50*	157·00
16·0	..	..	..	..	99·50*	162·00	130·15	162·00	155·08	162·00	93·80	162·40	118·38	162·00	144·36	162·00	155·88	160·75
16·5	..	..	..	..	..	..	..	..	..	..	97·25*	165·00	120·00	165·40	141·80	165·00	156·25	165·50
17·0	..	..	..	..	..	..	..	..	..	..	..	..	132·00	171·14	150·08	171·50	168·11	172·00
17 5	..	..	..	..	..	..	..	..	..	..	108·00*	177·00	138·00*	177·00	149·75*	177·00	170·50*	177·00

formed, i.e. September to December for I.-group and April to October for the later groups. It is clear that for each age-group there is a general tendency for the means of each calculated intermediate length to vary directly with the size of the fish: the larger individuals in any age-group will mostly have higher values for L_1, L_2, &c. and the smaller individuals the lower values.

TABLE 7
AS FOR TABLE 6, DATA OF 1938 YEAR-CLASS ONLY

Length-group (cm.)	II.			
	L_1	L	L_3	L
11·0	..	..	111·00	114·00
11·5	97·00*	118·00	114·38	117·92
12·0	93·11	122·67	116·94	121·39
12·5	97·14	127·57	122·00	127·44
13·0	102·60*	133·50	130·33*	133·33

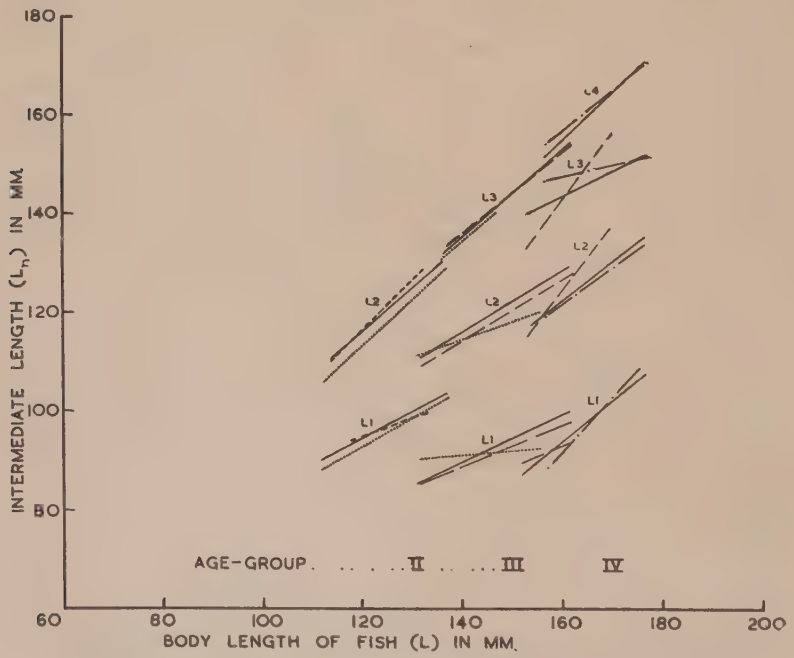

Fig. 6.—Data of Tables 6-10, regressions calculated; illustrating the relationship between calculated intermediate lengths (L_n) and length of fish (L), for all available age-groups for New South Wales north coast pilchard scales. Lines shown ———— are for all year-classes combined, — . — for 1935, — — for 1936, ····· for 1937 and – – – – for 1938 year-classes.

In Tables 7-10 these north coast data are given separately for the four year-classes (1935-1938) for which there is any significant information, and the whole of the evidence, for the separate broods and all combined, is set out graphically as a series of calculated regression lines in Fig. 6. The general

TABLE 8

AS FOR TABLE 6, DATA OF 1937 YEAR-CLASS ONLY

Length-group (cm.)	II				III					
	L_1	L	L_2	L	L_1	L	L_2	L	L_3	L
11·0	97·50*	112·00	110·00*	112·00	..	..	..	..	..	..
11·5	87·75	117·00	106·17	117·00	..	..	..	..	..	..
12·0	87·50	122·00	117·33*	122·00	..	..	..	..	..	..
12·5	89·33	126·83	118·50	126·83	..	..	..	..	..	..
13·0	105·67*	132·00	124·00*	132·00	85·67*	131·00	114·25*	131·25	..	..
13·5	106·20	137·00	131·00*	137·00	95·50*	135·50	113·33*	135·33	130·00*	136·00
14·0	..	..	..	..	..	..	111·00	140·00	139·00*	143·00
14·5	..	..	..	..	..	..	113·00*	147·00	138·50*	147·00
15·0	..	..	..	..	..	..	..	..	..	..
15·5	..	..	..	..	93·00*	156·00	123·50*	156·00	..	..

(Table 9 see page 52)

TABLE 10.

AS FOR TABLE 6, DATA OF 1935 YEAR-CLASS ONLY

Length-group (cm.)	IV							
	L_1	L	L_2	L	L_3	L	L_4	L
15·5	92·00*	157·00	123·80	157·00	146·50	157·00	152·50*	157·00
16·0	94·00*	162·00	118·00*	162·00	149·25*	162·00	157·33*	162·00
16·5	97·25*	165·00	120·00	165·50	141·80	165·00	156·25	165·50
17·0	..	..	130·50*	172·00	153·78	172·00	168·11	172·00
17·5	108·00*	177·00	138·00*	177·00	149·75*	177·00	170·50	177·00

pattern of the L_n/L relationship is quite unmistakable, and even shows up well for the data of the separate year-classes, considering that these were rather scanty on the whole. It is undoubtedly for this latter reason that the agreement between the regressions of the separate year-classes and the combination of them all is far from perfect in some cases, especially as regards the IV.-group, but in more than half the instances it is surprisingly good. The regression equations for the combined year-class data (it is unnecessary to cite those for the separate broods) are as follows:

II-group: $L_1 = 31{\cdot}36 + 0{\cdot}525L$
$L_2 = 5{\cdot}22 + 0{\cdot}915L$

III-group: $L_1 = 25{\cdot}23 + 0{\cdot}459L$
$L_2 = 27{\cdot}19 + 0{\cdot}629L$
$L_3 = 12{\cdot}79 + 0{\cdot}870L$

IV-group: $L_1 = 33{\cdot}30 + 0{\cdot}794L$
$L_2 = -4{\cdot}22 + 0{\cdot}788L$
$L_3 = 62{\cdot}66 + 0{\cdot}499L$
$L_4 = 0{\cdot}76 + 0{\cdot}960L$

Precisely the same type of relationship seems to hold for the south coast scale material, although, owing to relative scantiness of material in all cases but that of the I.-group, there are a number of cases in which it is not so

TABLE 9

AS FOR TABLE 6, DATA OF 1936 YEAR-CLASS ONLY

Length-group (cm.)	III						IV							
	L_1	L	L_2	L	L_3	L	L_1	L	L_2	L	L_3	L	L_4	L
13·0	88·00*	132·00	111·50*	132·00	..	..	..	..	..	..	..	..	..	..
13·5	84·00*	137·00	114·80	137·60	133·67*	137·33	..	..	..	..	..	..	..	..
14·0	94·50*	142·00	112·11	142·00	138·33	142·00	..	..	..	..	..	..	..	..
14·5	85·57	147·00	116·68	147·48	140·00	147·71	..	..	..	..	..	..	..	..
15·0	..	..	127·00*	151·50	144·00	151·67	89·00*	152·00	119·25*	153·50	135·00*	153·33	..	..
15·5	96·25*	157·00	125·33	157·00	149·43	157·00	..	..	..	..	..	..	..	..
16·0	99·50*	162·00	130·15	162·00	155·08	162·00	93·67*	162·67	118·75*	162·00	142·40	162·00	155·00	160·00
16·5	..	..	..	..	..	..	..	..	..	..	..	..	..	..
17·0	..	..	..	..	..	..	..	..	140·67*	170·00	157·67*	170·00	..	..

TABLE 11

AS FOR TABLE 6, SOUTH COAST DATA ONLY, ALL YEAR-CLASSES COMBINED

Length group (cm.)	I		II				III						IV							
	L_1	L	L_1	L	L_2	L	L_1	L	L_2	L	L_3	L	L_1	L	L_2	L	L_3	L	L_4	L
6·5	64·00*	68·00	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
7·0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
7·5	71·80	77·00	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
8·0	71·83	80·50	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
8·5	79·12	88·89	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
9·0	82·62	92·60	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
9·5	87·42	97·00	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
10·0	87·87	102·55	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
10·5	94·72	107·08	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
11·0	100·14	111·43	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
11·5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
12·0	..	..	93·83	122·00	111·20	120·60	..	..	..	..	..	..	..	..	..	..	..	..	..	..
12·5	..	..	88·00*	129·00	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
13·0	..	..	105·00*	132·00	121·00*	132·00	..	..	..	..	..	..	..	..	..	..	..	..	..	..
13·5	..	..	100·40	137·00	131·20	137·00	..	..	..	..	..	..	..	..	..	..	..	..	..	..
14·0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
14·5	..	..	..	..	..	..	..	..	..	..	142·00*	148·00	..	..	..	..	..	..	..	..
15·0	..	..	..	..	..	..	90·00*	150·00	117·67*	151·33	142·14	151·71	..	..	..	..	..	..	..	..
15·5	..	..	..	..	..	..	101·00*	159·00	113·50*	158·50	146·33	157·17	..	..	..	..	..	..	..	..
16·0	..	..	..	..	..	..	95·50*	160·00	116·00*	160·00	146·80	160·00	..	..	..	..	..	..	..	..
16·5	..	..	..	..	..	..	..	..	..	..	..	..	87·40	169·00	119·50*	169·00	..	..	159·40	167·00
17·0	..	..	..	..	..	..	..	..	..	..	..	..	97·00*	170·00	123·75*	171·00	150·71	171·14	167·91	171·82
17·5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
18·0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	155·33*	183·00	176·33*	183·00

obvious; and for this reason also, no attempt has been made to analyse the situation according to separate year-classes. The data for all broods combined are set out in Table 11. The regression equations are as follows:

$$\begin{aligned}
\text{I-group:}\quad & L_1 = 9{\cdot}30 + 0{\cdot}795L \\
\text{II-group:}\quad & L_1 = 15{\cdot}86 + 0{\cdot}623L \\
& L_2 = -28{\cdot}20 + 1{\cdot}149L \\
\text{III-group:}\quad & L_1 = -32{\cdot}04 + 0{\cdot}816L \\
& L_2 = 165{\cdot}70 - 0{\cdot}319L \\
& L_3 = 73{\cdot}17 + 0{\cdot}462L \\
\text{IV-group:}\quad & L_1 = -1546{\cdot}22 + 9{\cdot}666L \\
& L_2 = -235{\cdot}30 + 2{\cdot}100L \\
& L_3 = 83{\cdot}89 + 0{\cdot}391L \\
& L_4 = -9{\cdot}98 + 1{\cdot}022L
\end{aligned}$$

The position revealed here impressed itself upon the writer when reading the better type of scales. Its meaning is that the larger fish in every age-group have a higher apparent growth-rate than the smaller ones, so that the former seem not only to develop a lead in respect of growth in early life, but also to maintain it, more or less, throughout life. This is in marked contradistinction to what has been held for many other species of fish, for which some investigators believed they could demonstrate an effect of growth compensation by which individuals whose initial growth was good grew relatively less at a later stage, and those with poor initial growth grew relatively more, so that the pattern of growth-rate became eventually more uniform; for which reason this effect has been considered an adducent factor in the sense mentioned above. Not only is this adducent factor therefore absent in this case, but on the face of it the size of the fish should enter the list of dispersive factors.

The apparent effect of growth compensation was first referred to by Gilbert (1914) for the salmon *Oncorhynchus nerka*. A great deal of literature refers to its occurrence in the Atlantic herring, for which it was referred to in the first place by Watkin (1927, pp. 59-60), Ford (1928, pp. 248-9) and Farran (1928); although according to Van Oosten (1929, p. 371) the same thing was also shown earlier in some data published by Molander (1918). Hodgson (1929, pp. 55-57) admitted that it was apparent in his herring material but thought that the effect was not real. He considered that it was due, in the first place, to an assumption that all fish of a particular spawning would be of exactly the same age at the time of formation of any ring, whereas of course there would mostly be a variation of at least a few months; and in the second place, following upon this argument, that " with increase of age there is less ability to increase length and consequently the larger and older fish of any given growth period will grow less than the smaller and younger fish." Ford (1933, pp. 328-33) replied that this explanation was only partly acceptable, because " the ' curve of ability to grow ' may itself be subject to variation from fish to fish." Finally Runnström (1936, pp. 74-7) claimed that Hodgson's suggestion would not meet the case for the Norwegian herring, whose spawning period is limited, and believed that

the effect was real for this material, owing to the fact that the faster growing fish of southern origin, maturing earlier, have their subsequent growth retarded in consequence, while the slower growing individuals of northern origin do not suffer this until relatively late and in the meantime achieve a better growth-rate by migration to the more favorable southern areas. However, in this case the comparison is rather between different groups of fish than between individuals of the same group, which was more nearly the basis on which other authors have discussed the problem.

Among other references to this subject, there are the works of Van Oosten (1929, pp. 371-3) and Hile (1936, pp. 282-6) on the lake herring or cisco (*Leucichthys artedi*), for which they agreed that there was some compensation, although insufficient to obliterate completely, in its later years, any advantage in growth that a fish may have had in the earlier part of its life. Hile dealt with the matter again (1941, pp. 296-306) for the rock bass (*Ambloplites rupestris*), and found there was an apparent partial compensation in respect of the later life only; but he considered, like Hodgson, that this was probably largely illusory in this case because of variations in actual age of fish in the same brood, due to hatching at different times in the season, although not doubting that cases of real growth compensation do nevertheless exist in some species. Tiller (1943) described a compensatory effect for striped bass (*Roccus saxatilis*), although not completely diminishing the advantage or disadvantage initially held by the largest and smallest fish of a brood respectively. On the other hand Hubbs and Cooper (1935, pp. 676-9) for *Xenotis megalotis* and certain other sunfishes, McHugh (1942, p. 342) for the whitefish (*Prosopium williamsoni*), and Kesteven (1942, pp. 46-7) for mullet (*Mugil dobula*) all failed to discover any compensation phenomena. These authors mostly analysed the data on growth increments (T_1, T_2, &c.) in their treatments of the matter, rather than that on the intermediate lengths as has been done here, but it is obvious from Fig. 6 that the latter type of presentation is quite as adequate; the reason for resorting to it here was the fact that there were fewer actual readings of increments, due to missing rings.

In the present case the compensatory effect is not even apparent, the individuals which have an apparently good, medium, or bad growth at the time of formation of the first ring maintaining the same position as to relative growth at all later stages. Now since this growth, as measured by the values of the calculated intermediate lengths, is so obviously positively correlated with relative size in the age-group, there is no reason to look beyond the most obvious explanation, namely that the variations in L_1, L_2, &c. do not relate particularly to real differences in the growth of individuals at all, but merely to the somewhat different ages attained by them at the time of formation of any and every ring. In other words the individuals of a brood which yield higher L_n readings from their scales than do some others, do so because they are actually older fish, having been hatched in the same spawning season but at an earlier stage of it, just as was believed by Hodgson and Hile. It was stated in an earlier section of this study (II) that the maximum range of difference of size between the larvae of the same spawning season was of the order of 40 mm., and much the same applies to the fish almost throughout their life. The lowest and highest values recorded for L_1 in this study were 64 and 111 respectively, a difference of 47 mm.

for L_2 the corresponding values were 100 and 143, a difference of 43 mm.; for L_3, 129 and 165, with 36 mm.; and for L_4, 151 and 181 (which may not be the maximum possible), with 30 mm.

There has now been identified this one dispersive factor which seems to account alone very satisfactorily for the large range of variation in L_1, L_2, &c., and it appears to be a sufficient treatment of the problem simply to adjust the L_n means in Table 5 to bring them into line with the overall means of L for the different age-groups; and then, if evidence of Lee's Phenomenon or any similar consistent trend is still lacking, to obtain grand means for L_1, L_2, &c. based on all the data irrespective of age-group. This is not the ideal way to attack the problem, for which a multiple factor statistical analysis on the lines suggested by Kesteven (1946, p. 45), is preferable. Obviously this is not possible in this case, for which there has already been noted a highly uneven sampling with regard to locality, a regrettable omission of information as to sex, and inadequate data in respect of individual year-classes. Nevertheless it has been shown above that the sex factor is probably not important, and that such comparisons as can be made between the data of different broods reveal fairly good agreement.

One proceeds then to make the adjustments for fish-length referred to above, utilizing the regression equations set out above, and to observe what variations remain between age-groups for each major locality, and between the two localities themselves. Adapting Table 5 for this purpose, there results Table 12.

TABLE 12

MEANS OF CALCULATED INTERMEDIATE LENGTHS (L_1, L_2, ETC.) BY AGE-GROUPS, ALL YEAR-CLASSES COMBINED, NORTH AND SOUTH COASTS; VALUES (IN MM.) ADJUSTED TO ELIMINATE THE EFFECT OF FISH-LENGTH, SEE TEXT

—	Age-group.	L_1		L_2		L_3		L_4	
		No.	Mean	No.	Mean	No.	Mean	No.	Mean
North Coast ..	I	..	..	..	..	..	..	..	..
	II	51	96·01	75	117·90	..	..	..	..
	III	24	91·33	75	120·51	59	141·87	..	..
	IV	14	97·72	30	125·81	44	145·00	31	159·18
	Total	89	95·02	180	120·31	103	143.20	31	159·18
South Coast ..	I	101	86·80	..	..	..	..	..	..
	II	13	95·53	11	118·73	..	..	..	..
	III	7	95·06	6	116·01	19	145·13	..	..
	IV	(6)	(114·10)	6	125·42	10	151·05	24	165·57
	Total	121	88·22	23	119·77	29	147·17	24	165·57

In this table, for some of the adjusted mean values of L the alteration is upward in spite of the fact that the overall age-group mean of L was below the L value corresponding to the particular intermediate length in question, or vice versa. For example, for the north coast the L_1 value in respect of the II-group

was 94·14 in Table 5 for an L value of 124·31, whereas the overall L value for the II–group was less; one might therefore expect the corrected L_1 value to be less, whereas it is more. This is because some of the unadjusted L_n means were weighted by an unduly high number of observations towards the lower or upper ends of the ranges in question. On the whole it is seen that the adjustments make little difference, but the resulting L means probably represent the position more correctly; except for one or two cases as regards the scanty south coast material, where it is obvious that the new figures will be no more reliable than the original ones if not less so, and one case (L_1 in the IV–group) where the adjustment produces a completely misleading figure which has to be omitted. There is no evidence of Lee's Phenomenon or any other consistent trend in the L_n means for different age-groups, and it is thus permissible to regard them as randomly distributed about a series of grand means of L_1, L_2, &c. based on all observations irrespective of age-group. These means are shown in Table 12 for the north and south coast data respectively: for L_1, L_2, L_3, and L_4 they are 95, 120, 143, and 159 mm. for the north coast fish, and 88, 120, 147, and 166 mm. for the south. These are the most reliable figures that can be obtained to describe the average sizes of pilchards at the time of formation of the first four annual rings respectively, i.e. at ages of approximately $1\frac{1}{4}$, 2, 3, and 4 years.

It is extremely doubtful whether the differences between these two sets of figures constitute sufficient grounds for postulating a different growth-rate in each locality. In view of the fact that the data are far from being as adequate as one would like, and that circumstances of their collection do not permit a really full analysis of the variation in growth, all that can be said is that if there are any such actual differences they are quite small. With this point in mind it is permissible to combine the two sets of figures to obtain (as weighted means) a single series of values for the New South Wales coast as a whole, which was the object of this section of the study. These are:

$$L_1 = 91{\cdot}10 \text{ mm.}$$
$$L_2 = 120{\cdot}24 \text{ mm.}$$
$$L_3 = 144{\cdot}08 \text{ mm.}$$
$$L_4 = 161{\cdot}97 \text{ mm.}$$

These accord extremely well with the modes of the four age-groups as revealed by the length frequency studies (see Section II).

From this final scale of mean L_n values, those for the growth-increments may be taken to be approximately as follows:

$$T_1 = 91 \text{ mm.}$$
$$T_2 = 29 \text{ mm.}$$
$$T_3 = 24 \text{ mm.}$$
$$T_4 = 18 \text{ mm.}$$

These values are reasonable in that they indicate a gradual tapering-off of growth in the successive years of life, which is the usual pattern of growth-rate in marine fishes.

3. The Probable Circumstances of Ring-formation

In an earlier section (III, 1*a*) it was noticed that in this material at least two kinds of age-rings could be distinguished. One of those groups was observed to resemble closely the category of "spawning marks" recognized in Caspian shads by Zamakhaev (1940) and Tchougounova (1940). It is of some interest to investigate the possibility that these particular rings may register spawnings in the Australian pilchard.

The argument of the above-mentioned writers is summarized below, as these papers may not have been available, in translation, to many workers.

1. There are two main kinds of rings which are called the "yearly" and the "spawning" rings, and the appearance of the latter suggests a sharp break in the scale material (at least in the upper striated layer) and a subsequent resumption of growth. This is shown mainly on the sides (see references given previously).

2. In mature or ripening fish, one ring of each kind is formed each year, at much the same season, but with the yearly ring generally appearing earlier than the spawning ring (which often obliterates it). Collections of scales from fish of progressively riper stages show that the proportion of those with spawning rings newly formed at the margins rises to a maximum when the fish are mostly spent (Tchougounova, pp. 29-32, 37; Zamakhaev, pp. 12-3).

3. Immature specimens do not appear to have been studied, but as the first two or three rings on most shad scales are of the ordinary yearly type, with no association with or interference by spawning marks, and since it is implied that in these species most of the fish are by other evidence immature for the first two or three years (though this was not specifically shown), the conclusion is that spawning rings are not formed on the scales of virgin fish (Tchougounova, p. 26).

4. Spawning rings are not formed on all scales of a fish, nor with similar distinctness on all scales on which they occur, the most conspicuous breaks generally appearing on those from the middle of the flank; whereas the appearance of yearly rings on the scales of different body areas appears to be more uniform (Zamakhaev, pp. 15-6; Tchougounova, p. 37).

5. "It is natural that a sudden loss of subcutaneous fat causes a shrinking of the skin . . . . The pressure of the skin due to the loss of subcutaneous fat holds the scale firmly in the skin pocket. An increase of this pressure, however, produces probably a displacement and then breaks of the borders of the scale 'lamina.' It is quite natural that the breaking of the borders is strongest in the central part of the body of the shad, below the dorsal fin, because the greatest amount of subcutaneous fat is accumulated in this zone and the fish has its greatest girth there. A rapid loss of fat in the pre-spawning and spawning periods takes place also with the Caspian shads" (Zamakhaev, pp. 16-7).

This sort of hypothesis is not new. The first author to describe a "spawning mark" from any species was Johnston (1905), for the salmon *Salmo salar,* and he stated (p. 65): "A fish in the process of spawning falls off in weight and girth . . . . The skin readily adapts itself to the change,

carrying the scale rows with it, but the compression of imbricated scales tends to increase the amount of overlap, and from this or dermic influences we find that their margins become ragged and frayed. When the new growth is added . . . . the regularity of its structure is distorted to fill up the damaged portions of the other part of the scale, with the result that a more or less distinct junction is visible. This I call the spawning mark . . . ." It will be seen that Johnston had in mind a process essentially similar to that by which Zamakhaev assumes the shad spawning marks are formed, though the latter author does not mention the former's work. Johnston's views on the significance and origin of the salmon spawning mark have not, however, been generally accepted by subsequent workers. Masterman (1913, pp. 30-1) and Crichton (1935) produced evidence which they regarded as disposing of this mechanical hypothesis, but which does not seem to do so as far as the alternative suggestion about "dermic influences", especially considered in the light of Zamakhaev's remarks, is concerned. These and other authors have mostly regarded some form of scale absorption as the cause, though not necessarily connected directly with the spawning process (Van Someren 1937). It has been shown definitely that the marks can occur in fish that have not yet spawned, although they are confined to those that are maturing.

It is not proposed to express any opinion here as to which explanation best meets the case of the spawning marks on the clupeid (shad and pilchard) scales. At least there is no reason to dismiss the mechanical fracture hypothesis out of hand for the Caspian shad material, and the markings on the Australian pilchard scales are very similar and in both cases they are not very much like those that occur with salmonoids. It is hoped to investigate the question later with a more adequate amount of pilchard material.

One may now attempt to show directly that these marks on the pilchard scales, that so closely resemble what may be regarded as proven indications of spawning or advanced maturity in the Caspian shad material, have actually this significance for the pilchard. This cannot be shown quite as convincingly as might be thought possible, largely because of difficulties which have been encountered in the study of sexual maturity in the fish themselves. However, virtually all the indications are that these rings do indicate the achievement or approach of the spawning condition.

The study of maturity in the New South Wales pilchard was complicated by the fact that the overwhelming bulk of fish that are available are either immature (virgin), spent, or spent recovering, and quite considerable difficulties were often encountered in distinguishing between these. The more recognizable filling and full stages were only rarely met, and the typical winter surface shoals consist of fish which, apart from some proportion of virgins, are almost entirely spent. (That is to say, even in the spawning season the fish mostly do not school at the surface until reproduction is complete.) Now a recently spent pilchard is not hard to distinguish, because of the bloodshot flaccid appearance of the gonads and scattered residual large ova (in females), but much more difficulty attaches to the later recovering spents, because the organs are apt to shrink away almost to the size of those in virgins, the bloodshot appearance is gradually lost, and (especially in preserved material)

it is often very hard to distinguish between specimens that have never matured and those whose gonads have returned to the "resting" stage. The writer was able to discriminate properly between these stages as time went on, but most of the older fish were collected at an early stage in the investigation, and many of the maturity determinations upon them are somewhat suspect, and it has not been possible, because of the lack of any organized fishing, to duplicate most of the material. Therefore the writer cannot produce any reliable quantitative tabulations to indicate proportions of mature or immature fish for successive size- and age-groups, but some very general findings may be stated with confidence. It is practically certain that no fish becomes mature before its second year. Of the II-group pilchards some are mature, some not, and all that can be said is that the proportion which does spawn at this age is quite considerable, possibly of the order of 50 per cent., perhaps rather more or less; the proportion of matures seems definitely to rise, as it should, in the successively larger sizes of fish. The III-group consists for the greater part of mature pilchards, but a few at the smaller sizes do not spawn. Finally, from all the evidence, there are no fish which are still virgins at the age of four years.

Now a complete examination of the scale material showed, first of all, that no definite rings of the actual type in question, i.e. the extremely sharp conspicuous ones resembling breaks with a distinct zone beyond with no or only scattered striae, occur in the entire array of first annual rings or secondary rings associated with those. There are a few that are superficially like them, but upon close examination (see Section III, 1*a*) they do not seem to be the same, being mostly not so sharp or generally conspicuous, or lacking the outside unstriated zone, or both. All the rings of the presumed spawning-mark type that occur in the pilchard material are formed at two years of age or more, and thus all more or less in the winter season, i.e. when spawning takes place.

The next step is to discover the proportions of the totals of second, third, and subsequent rings that are of the true spawning-mark type. It would not be hard to find these proportions in respect of all the rings of each age that were definitely recorded, but these would probably be on the high side, for the second ring at least, because of omitting that considerable number of scales which by all indications should have borne rings but did not show them. Possibly all or nearly all such scales could be counted as negative from the present standpoint (on the grounds that the sharp spawning marks would appear even if the others did not), but then there is the difficulty that the age of the fish to which these non-ringed scales refer is in doubt in many individual cases. Another difficulty is that the spawning mark nearly always follows the annual ring of the ordinary type*, and where a scale bears a ring of the latter kind close to the margin (or no perceptible ring at all), that is no guarantee that a spawning mark would not have been formed within a short time if the fish had lived. Thus the only reliable way to proceed is to

* Murat (1935, p. 126) quotes De Buen (1925, references unavailable to the present author) as believing that, in cases of double winter rings in the European pilchard, the earlier marks indicated the spawning and the second the winter slackening of growth. The conclusion reached in the present work is the opposite of this.

consider for the second annual ring only those that occur on definite III-, IV- and V-group-scales, for the third ring only those that occur on IV- and V-group scales (also some which are III plus), and so on. Scales that are partly or wholly regenerated must be excluded from these counts, as even when rings are visible on them it is often very hard to decide what kind they are. Unmeasurable and missing rings should be included, the latter to be counted as of the ordinary (non-spawning-mark) type on the basis of the argument above.

From this procedure, it is found that out of 176 observations on the second ring, 66 (38 per cent.) refer to the spawning-mark type and 110 do not. The latter figure includes 55 cases in which the ring was either unmeasurable or absent altogether, i.e. cases for which no values of L_2 had been entered. The observations for which such values are available reveal broadly the expected trend, the proportions of spawning marks tending to rise gradually in increasing intervals of L_2, but the actual percentages are of no significance. For the third ring there are 84 observations, 58 (69 per cent.) of which are of the spawning-mark type and 26 (including 14 cases of unmeasurable or absent rings) not, and the general trend with respect to values of L_3 is as above. The occurrences of the fourth ring cannot be analysed in this way since there are so few data for the V-group, but the indications from the scale readings as a whole are that they are overwhelmingly, though not entirely, of the spawning-mark type.

Comparing these rough estimates of the proportions of rings of successive age which are of the spawning-mark type, with the above very crude estimates of the proportions of fish which are mature in the corresponding age-groups, a fair measure of correspondence is seen. The percentages of spawning-mark rings for the third and fourth rings, and possibly for the second too, are somewhat lower than would be expected, but considering the virtually non-quantitative character of the analysis of maturity, and the rather few data available for the analysis of ring-types, it is considered that the two characters in question are correlated in the same way as for the Caspian shads. It must be borne in mind that any attempt to classify rings by eye must be somewhat subjective. Another difficulty about this process, and the comparison with the maturity data to which the results are applied, is that although the presence of a spawning ring definitely seems to indicate a maturing fish, its absence does not necessarily indicate an immature one, because there are a few cases in which several scales from the same fish were compared and some showed the mark quite clearly and others did not. This factor probably operated to reduce the percentages of spawning marks in the above series of counts.

This last observation recalls that these rings are not found on all scales of the Caspian shads either, which was explained by Zamakhaev on the argument that they resulted from a loss of fat in the fish in the maturing and spawning stages, and that this was greatest in the middle of the body. New South Wales pilchards are also much fatter in the summer, before and between spawnings, than they are at the spawning time (see Blackburn 1941, pp. 44-5). This is consistent with Zamakhaev's theory of the cause of formation of the spawning marks for the Caspian shads, but, as stated above, it is not desired to assert at this stage that this type of explanation is the correct one in the

case of the pilchard. At any rate the formation of the spawning ring does not necessarily depend upon the actual shedding of the genital products, any more than it does for the shads or *Salmo salar,* because there are a few scales in the collections that bear these marks which definitely refer to individual fish which had not got beyond the filling or full stage. It is a weakness of this study that these indications as to maturity or otherwise on the scales could not be checked against the observed sexual condition of the individual fish in most cases. This was partly because the sets of scales as collected and mounted refer mostly to size-groups and not to the separate fish, but also largely because of the above-mentioned difficulties in deciding exactly what was the condition of many of the fish. However, there was no instance of a true spawning mark on a scale from a definite virgin fish.

Thus, while actual proof is lacking, all the available evidence strongly suggests that these particular rings are valid indications of maturity in the fishes on whose scales they occur. However, the absence of such a mark upon a scale does not necessarily mean that the fish is immature.

As regards rings of the second main type occurring on the pilchard scales, an explanation of their occurrence can be sought along fairly well-established lines. These are the plain, much less conspicuous rings which seem to derive their appearance from minor breaks and waviness in the striae (Section III, 1*a*). These comprise all the secondary and first annual rings (except those few that somewhat resemble the spawning marks) and all those of the second and subsequent annual rings which are not of the spawning-mark type. It seems possible to explain the mechanism by which these rings are formed by reference to much thorough work by other authors upon the structure of the clupeid scale, all of which can reasonably be assumed to apply to that of the Australian pilchard. The authors to whom reference is made are Lea (1919), Savage (1919), and Lee (1920), who dealt with the Atlantic herring; Paget (1920), who worked on the herring and *Clupea reevesi*; Robertson (1933), who studied the herring and sprat; Murat (1935), who was concerned with the Mediterranean pilchard; and Graham (1929*a*). In general their observations are in good agreement, and the general theory as to ring formation in clupeid scales as it seems to stand today can be summarized as follows:—

1. " Two layers enter into the composition of the scale: an upper, which is apparently homogeneous, and a lower, lamellated one. The upper layer is raised into ridges (striations) in its anterior part . . . . The lamellae of the lower layer . . . . are continually being laid down, the lowest being the most recent as well as the greatest in area; thus the lower layer or the scale has the form of a very shallow cone " (Savage 1919, p. 4; see also Lea 1919, pp. 86-9; and Paget 1920, pp. 17-8).

2. " The increase in area of a lamella from that formed immediately before it depends normally upon the period of the year when it is laid down; . . . . the increase is greatest in the early part of the summer, and becomes gradually less towards winter " (Savage, p. 4). That is to say, the most recent or lowest lamella of a scale will never be less in area than the one above it, but if formed in the winter (or whenever is the season of slowest

growth of the fish) it will be no more or very little greater in extent, whereas at other periods it will tend to be substantially more in area (see also Lea, pp. 90-1; Paget, loc. cit.; Robertson, pp. 360-1; Murat, pp. 112-6). "The result would be that the scale . . . . would have an upper layer with a slightly variable slope. These variations in slope having the character of terraces or low cliffs, might, by slight distortion such as a further flattening of the cone, become ridges possibly accompanied by an external *fossa,* representing the top and bottom of such a distorted cliff" (Robertson. p. 361). Or the lamellae formed at the season of slowest growth may bend upwards slightly so as to form, at each such period, a ridge on the upper surface of the scale (Paget, p. 18).

3. The striated (calcareous) upper layer of the scale (anterior part), which is secreted by a different group of cells, seems to lag a little behind the formation of the lower fibrillar part, so that its area is not quite as large, at any rate at the season of slowest growth (see Lee, pp. 6-8; also Savage, p. 8, and Paget, loc. cit.).

4. It follows that the striated layer (which is itself of uniform thickness throughout, see Lea, p. 89, and Paget, p. 18) takes, as it were, the mould of the cliffs and ridges formed as mentioned above on the upper surface of the fibrillar part of the scale at the seasons of slow growth. This causes the striae to appear kinked or waved, owing to a perspective effect, when the scale is viewed from above (see Robertson).

5. This does not explain the small local breaks in the striations that are also an important feature in connection with the formation of these rings, especially in the pilchard scales. The most plausible line of explanation seems to be on lines suggested by Graham (p. 43), who says: "At the period when the winter-ring is formed the etched surface is not formed, for the reduction of the calcium-secretion-rate to zero would mean in practice an equilibrium which in slightly varying conditions would cause some of the surface to be reabsorbed. Sometimes this reabsorption results in a furrow, sometimes merely in the loss of striations. On the resumption of growth new deposition occurs as usual on the projecting portion of the laminar layer". This kind of explanation would probably be valid even if the secretion of calcareous material did not completely cease*.

To meet the case of these rings in the pilchard scales along the lines of this theory, it would be necessary to show that the growth of the fish is reduced at the various periods at which these marks are formed, or to suggest some factors that would be likely to cause such reduction. This can only be done in part at present. As regards the rings of this type that are formed in the winter, i.e. all the second, third, and possibly subsequent annual rings that are not of the spawning-mark type, there is the evidence from studies with the Petersen method that the growth of the pilchard is indeed very slow at this season. The most obvious explanation is that which postulates a shortage

* In a recent study on the European sprat scale, Molander (1946) has stated that the "transparent" zones generally regarded as "winter rings" really represent the beginning of faster growth, whereas the real winter or diminished-growth formation is represented by a concentric band of closely approximated sections of the striae just inside the transparent zone.

of suitable food. Determinations of mean volume of stomach contents were made for most of the samples handled, but there were very few of these available for other periods of the year besides the general winter season, and so no reliable comparison of seasonal rates of feeding can be made. Some work has been done on the identification of the principal organisims found in the New South Wales pilchard stomachs, and seasonal fluctuations in these*, and this indicates that the groups that are most fed on seem to be usually least abundant in the general winter season, at least the earlier part of it, which is more or less in line with the suggested hypothesis. The principal groups concerned are ostracods, copepods, euphausiaceans, mysidaceans and various other malacostraca, the latter mostly as young stages. However, there might be other factors responsible, perhaps more immediately so, for the formation of the rings in question, as discussed below.

With regard to what has here been called the first annual ring the question is more difficult, because these rings are formed in the spring, when the growth of the fish is extremely fast. However, it is possible that, although this period of the fish's life is on the whole one of fast development, at least most of the individuals do suffer a brief check in growth. This becomes rather more plausible when it is considered that at about this stage the fish undergo what is probably the most important single change in their manner of living, for the whole of their lives subsequent to the postlarval stage. As shown in more detail later, the pilchards are then leaving or preparing to leave, for the open sea waters, the bay and the inlet environment in which they have passed most of the previous year. Furthermore, this migration seems to involve them typically becoming congregated into large and dense shoals. One can easily imagine that such a change as this, involving an alteration of actual environment and of manner of living, could very well result in a sudden brief diminution of growth-rate. Actually it is more likely that the assumption of the shoaling habit, rather than the movement out to sea, is the critical factor, because fish from a shoal netted in November 1939, quite high up the Wagonga Inlet, mostly had the ring in question clearly formed.

Indeed this particular hypothesis, in which the emphasis is placed upon the assumption of the schooling habit, becomes even more attractive when it is considered that it might also explain the formation of the similar rings that are formed in the winter, which might then be regarded as a sudden check in growth due to the assumption of the shoaling habit, rather than a slowing-down due to food shortage, as suggested above. This would explain one rather peculiar feature of the appearance of these rings, namely that they may already be found some little distance inside the margin at almost any time during the general winter season, even as early as April and May. That is to say, they are apparently not formed as a result of a gradual process involving the whole season or any other lengthy period of time, as one would expect if a simple reduction in general food supply was the basic factor; in fact the suggestion is that they are formed suddenly and, on the whole, at an early stage of the general winter season. Now it was mentioned above that, at least as far as mature fish are concerned, the pilchards do not appear to form dense

* By the writer's colleague K. Sheard, who kindly provided the information summarized here.

shoals at the surface until after spawning; but if it could be shown that there were similar congregations below the surface at the spawning and pre-spawning stages*, whereas before that the fish were more dispersed, then it might be argued that the scale-rings resulted from a sudden and brief check in growth-rate associated in some way with the fish becoming grouped into schools. Actually this effect could itself be basically one connected with nutrition, for example through increased competition per unit area for a food supply which might be diminishing in any case. (There seems little reason to doubt that the winter schools are primarily spawning congregations, though involving some immature fish.) As it happens, there is virtually no evidence for (or against) these suggestions as to when the fish congregate into shoals at sea, and thus they are quite hypothetical at this stage. It is also hard to understand quite how the ring could be completely formed in a portion of the season only, when according to evidence from length frequencies the growth-rate of the fish is slow over the whole of it, bearing in mind the theory of ring-formation set out above. Nevertheless the facts appear to be thus, and it does not seem utterly impossible to reconcile the two effects.

As for the secondary rings, they must be regarded also as usually arising from a temporary reduction of growth-rate in the individual fish. These particular out-of-season growth-rate effects, however, affect a minority of the population only, and it is this that gives them their "secondary" character in respect of utility for age-determination purposes. It is quite easy to think of a number of possible vicissitudes which could produce this effect in certain individual fish only, especially as most of these rings are formed during the year or so of inlet life when the fish are probably rather dispersed, and could encounter a great variety of environmental influences. Savage (1919, p. 5) showed that at least some of the "false" rings in herring scales were associated with reduced growth of the lamellae in somewhat the same way as for the annual rings.

It remains to mention the relatively small number of first annual rings that somewhat resemble the spawning marks. The most striking case is that shown in Plate 2, Fig. 1. However, this scale was one of a set of six from the same fish, and only one of the other five showed anything remotely resembling the appearance of this ring, and that on a very much reduced scale, while the remaining four had either a plain ring only or showed none clearly at all. This fact, together with the unusual appearance of the ring, suggests some injury to this particular scale (which could possibly have affected a few of the adjacent ones in less degree) more than anything else. The other examples are all much less spectacular and could easily be due to the striae crossing an unusually sharp cliff or ridge on the surface of the fibrillar layer, and/or being reabsorbed locally to an unusually great extent.

Summarizing, it has been shown that two main kinds of scale rings can be distinguished by their general appearance. One type seems to be associated in some way with advancing sexual maturity, and although the presence of such marks does not necessarily indicate the actual spawning, but rather

* According to Kishinouye (1907, p. 81) this is actually what happens with the pilchard of Japanese waters.

its imminence, it is convenient to refer to them as " spawning rings ", as used hitherto in the literature for other species. The other sort of ring is probably associated with diminution of growth in the scale material and hence doubtless of the fish, and although it is not possible to distinguish different groups in this category by appearance, there are definitely at least three separate kinds considered in terms of their significance as a register of events in the life of the pilchard. These are: (1) the first annual rings, which seem to be associated in some way with a major movement of the pilchards from the inlet waters to the open sea, and which it is convenient to call " migratory rings "; (2) the second and subsequent annual rings (as distinct from the " spawning rings " of those years, with which, when both occur, there is some interaction), which are formed at regular intervals after the fish has assumed its open sea phase of life, and can be called simply " yearly rings "; and (3) the " secondary rings ", which occur on the scales of only a minority of individuals, mostly in respect of the inshore (pre-migratory) phase. The rings of at least groups (1) and (2) seem to be formed rather suddenly and quickly, and possibly both might be re-combined under the more explicit heading of " schooling rings ". The spawning rings are the most conspicuous and are not often omitted, so that the scales of older fish are on the whole more easily read than those of younger ones.

All this accords rather well with the notions of Lea (1929), Runnström (1936), and others as to the possibility of obtaining from the scale-readings more information about the life-history of the individual fish, or information of a more explicit kind, than had been sought by most previous workers. This idea really goes back to Johnston in 1905, and is thus practically as old as the technique itself. The writer feels that further work of this kind would be valuable, although it might prove to be of direct practical value in some species only.

Furthermore, studies like these emphasize some of the complexity of scale-reading and thus provide a deterrent to any tendency to oversimplification of theory or mechanical approach in practice, which has characterized a good deal of this work in the past. Actually there is no reason whatever to assume in advance that the ring-pattern will present that regularity which is of the most convenience to the scale-reader, although this probably does quite often happen. On the contrary the rings on the scales of one and the same species may vary in appearance, origin, time of formation, and the regularity with which they occur from fish to fish, and the task of the investigator is then to discover those which occur most regularly within the population of each stage, and establish the significance of these in respect of time (and origin if possible), and then proceed along the lines of the more conventional scale-reading practice. This means that any scale-reading work, certainly at the initial stages and thereafter unless it is found that the ring-pattern is indeed fairly regular and simple, cannot be expected to be done competently by any one who is not familiar with the general biology of the fish. It seems necessary to state this explicitly, because there will often be a temptation to allow this work, which on the face of it is so mechanical, to be handled as a routine. Apparently this tendency has reached alarming proportions in the United States, as witness the observations of Van Oosten

(1941, pp. 197-8) that "our research workers on fresh-water fishes have taken the scale method too much for granted" and that "it is time to halt the promiscuous use of the scale method in fishery research and management".

4. Conclusions

The important conclusions to be drawn from the scale studies, as to the specific questions of the age and growth-rate of the pilchard, are as follows:

1. The New South Wales pilchards average about 91, 120, 144, and 162 mm. of body length at ages approximately 1¼, 2, 3, and 4 years respectively. A few larger fish live for at least 5 or 6 years.

2. The age-groups I and II overlap at sizes of fish between 10·0 and 11·0 cm., inclusive; the II- and III-groups between 12·5 and 14·0 cm.; and the III.- and IV.-groups between 15·0 and 16·5 cm. Possibly the overlapping is a little more extensive.

3. The differences in growth-rate between the fish of the north and south coast localities, if any, are very small, and the same probably applies to the pilchards of different year-classes.

4. Some fish seem to have a substantially higher growth-rate than others throughout life, but these seem to be mostly the older individuals of a year-brood, so that the effect is more apparent than real.

It will be seen that these results agree very well, so far as they are comparable, with those that were obtained from the studies with the Petersen method (cf. Section II).

IV. STUDIES WITH THE OTOLITH METHOD

It is unnecessary to say very much about this section of the work. The otoliths, which range in length up to about 3·6 mm. in respect of fish of 17·0 cm., were examined whole, immersed in xylol. With reflected light there could generally be seen at least sections of dark lines running more or less parallel with the outline of the otolith, in the usual manner of age-rings in the otoliths of other species, and these were considered to represent such markings.

However, when an attempt was made to establish the number of these marks for each otolith, it was found that this task exceeded the scale-reading work in difficulty, and so this entire line of work was eventually abandoned, Taken collectively the otoliths of a particular size-group did seem mostly to indicate the age or ages that the results of the length-frequency and scale work had shown was appropriate for the corresponding fish, but little confidence could be placed in the correctness of any individual reading. Moreover it seemed that even this limited measure of agreement was at least partly due to a sort of involuntary rationalization of the data which tended to bring them into line with what it was already known, from the other lines of work, the general results should be.

Among the difficulties which beset this work were those arising from secondary and omitted "rings", similarly to the scales. The inner one or two rings were also generally hard to see, and only a few of them could be

traced clearly for any great distance. Again, there was constant trouble in respect of the edge of the structure and the possible presence or absence of a ring there, because the pilchard otolith is rather flat and quite thin at the margin, so that this portion is typically translucent and appears as a dark band which may easily be taken for an age-ring. When to these difficulties are added those associated with dissecting out and storing and handling such small fragile structures, it is clear that the otoliths are not to be compared with the scales in respect of their utility for age-studies on the Australian pilchard.

Some idea of these can be gathered from Plate 8, Fig. 2, which shows a specimen that was clearer than most. It is from an 11·5 cm. fish taken in May, which, judging from the results of both the length-frequency and scale studies, would certainly be two years of age or almost so, and there are indeed two indubitable rings upon this otolith. However, the inner one is really quite faint, and also there is towards the margin the dark translucent zone mentioned above, which is in this case due merely to the thinness of the edge, although it might at first sight be taken for an age-ring; the more so because, as in this and other otoliths, part of the extreme edge of the structure may also reflect some light (depending upon the position of its source with relation to the specimen) and so suggest the beginning of a zone of faster growth outside a ring, all of which is actually an illusion.

Walford and Mosher (1943*a*) worked with otoliths as well as scales from the North American pilchard, and obtained good to moderate agreement between the two independent series of determinations. This work referred to fish of up to three years only, and is not mentioned in connection with a later study by these authors on older fish (1943*b*), for which apparently only scales were used. Judging from the photographs, these otoliths showed the rings much more clearly than did those which the present writer has studied. Some other workers (e.g. Fage 1913) have referred to studies on the otoliths of the pilchards of Europe, but these do not appear to have been extensive.

V. COMPARISON WITH THE GROWTH-RATES OF PILCHARDS OVERSEAS

It is now of interest, particularly because of the bearing it may have upon the general appraisal of the properties of the environment, to try to compare the growth-rate of the pilchard of New South Wales with those of other members of the genus *Sardinops* and closely related *Sardina* in other parts of the world. For these other pilchard (or "sardine") species there is published evidence relating to *Sardina pilchardus* from Europe and the Mediterranean, *Sardinops caerulea* from Pacific North America, and *S. melanosticta* from Pacific Asia. The growth-rates of the two other species, *Sardinops sagax* and *S. ocellata,* from Pacific South America and South Africa respectively, do not seem to have received any attention. *Sardinops dakini* Whitley from Thursday Island is a little-known species which is a very doubtful member of this genus, and would probably be referred to *Sardinella* by most workers (see Whitley 1940, pp. 401-2).

There is a fairly extensive literature on the age and growth of the above-mentioned three species, especially the European one, most of which is listed in the bibliographies by Mohr (1927, 1930, 1934) and Wheeler (1931). However, a good deal of it relates to some early and mostly somewhat crude work based on length frequencies. A good deal has also been done with scales (and a little with otoliths), but some of this work is of rather indifferent quality and so it is more difficult to make satisfactory comparisons of growth between species (or groupings of lower rank) than might be thought. For instance nearly all these workers obtained their calculated intermediate lengths by the direct proportion formula, without any attempt being made, so far as the writer can discover from the literature available, to show that this type of L/S connection actually held for their material. Ramalho and Boto (1931), Murat (1935), and Aikawa (1940), who did investigate this matter, all found that an equation of the $L = A + B.S.$ type was the more appropriate, and this was also in part the finding of Walford and Mosher (1943*b*). Furthermore, most of the investigators seem to have treated the critical question of the season of formation of the age-rings rather casually, some of them speaking of "winter rings" without producing any real evidence to show that any ring is formed at that season, while others seem to have established this point satisfactorily for some age-marks but not necessarily for all. In fact, practically all these writers have considered every ring as formed in the general winter season, whereas from the foregoing studies on the closely related Australian species one might very well doubt that this would always be so; especially as some of the age-rings might easily be spawning marks of the type found in the Australian material, and some of the overseas pilchards spawn in the summer. Mention of this leads also to the difficulties of comparing growth-rates, based on calculated intermediate lengths from scales, when some populations are winter and some summer spawners, assuming that the rings are actually winter rings. For instance, Le Danois (1929) attempted to demonstrate differences in growth-rate between three European pilchard populations by representing L_1, L_2, etc. as lengths attained at similar ages, although previous investigators had shown that two of these groups were summer spawners for which L_1, for example, would represent the size at much less than one year if the ring was formed in winter.

Taking *Sardina pilchardus* first, one begins with a consideration of its growth-rate in the Mediterranean. Fage (1913) investigated it on the French coast, and nominated for L_1, L_2, L_3, L_4, and L_5 values of about 8·0, 12·0, 14·0, 14·5, and 16·0 cm. of *total length* respectively. Like most other European workers on the pilchard, Fage actually obtained his estimates of mean size-for-age in part from measurement of fish of known age, as well as from calculated intermediate lengths. For Algerian waters Murat (loc. cit.) obtained higher L_n values, about 11·0, 14·5, 15·5 and 16·0 cm. for the first four rings. The only other such work of much importance in this region was also done, for fish of various localities, by Fage (1920)*; the estimates of L_n seem to fall rather between the two series above. Since the general spawning season in the Mediterranean is in the winter (the main authority on this point, as for

* Not available to the writer; quoted in De Buen (1937).

pilchard spawning seasons in other European waters, is De Buen (1935, pp. 112-5)) it follows that the figures given probably do really approximate to the mean lengths of age of 1, 2, 3, and so on.

In the Atlantic, the pilchards seem again to be more or less winter spawners as far north as about the River Loire in France. A good deal of work has been done on the growth of the fish in various regions here, by Hjort (1913, pp. 58-67), Fage (1920), De Buen (1925, 1929), Ramalho (1927, 1933), Arné (1928), Belloc (1932), Desbrosses (1933), and Sanchez (1933)*. Most of it, in fact most of the work on the growth of European pilchards generally, has been reviewed by De Buen (1937, pp. 387-93). The values given for L_1, L_2, etc., which can be accepted as rough estimates of size (total length) at actual ages of 1 year, 2 years, etc., show a substantial variation between authors, whose findings fall into two series within each of which there is reasonable agreement. From most of the accounts, average size at the first six anniversaries of birth would be about 11·0 to 13·0; 15·0 to 16·5; 16·5 to 18·0; 17·5 to 19·0; 19·0 to 20·0; and 20·0 to 21·0 cm. in total length. According, however, to Belloc, Desbrosses, and Sanchez the figures would be about 8·5 to 9·5; 12·5 to 13·5; 14·5 to 16·5; 16·5 to 17·5; and 18 cm. Such differences as these may be due, at least in part, to actual differences in age at the time of formation of the rings, caused by some individuals or groups having been spawned early and others late in the same general season, which varies somewhat in different districts.

The next region it is convenient to take is that of Brittany in France. Evidence as to growth-rate has been published by Fage (1920) and Le Gall (1928*a*; 1928*b*; 1930). The figures for L_1, L_2 etc. are reasonably well in accord, namely about 10·0 to 12·0; 15·0 to 15·5; 17·0; 18·0 and 18·5 cm. in total length respectively. However, in this region the general pilchard spawning season is the summer and therefore, if the rings for which these intermediate lengths are calculated are winter rings as they are claimed to be, one would have to think of the lengths as representing ages of about $\frac{1}{2}$, $1\frac{1}{2}$, $2\frac{1}{2}$, etc. years. Actually the average ages might be a little more, say by three months, in each case, because those spawned in the early part of the season (spring) would be perhaps about nine months old at the first winter, while those spawned in the later part (autumn) would possibly have no scales at the first winter and thus not receive their first ring-inscription until the following one, at an age of perhaps fifteen months (see Le Gall 1939).

For the waters of Britain there are data from Hjort (1913), Storrow (1915), and Le Gall (1928*a*, 1928*b*), and there may be included here some similar figures from the last author for pilchards of Boulogne across the Dover Straits. There is considerable variation as regards L_1 but for the subsequent figures the agreement is fairly good. Approximate values for L_1 to L_{14} are: 9·5 (or less) to 12·5; 16·0 to 17·5; 19·5 to 21·0; 21·0 to 22·0; 22·5; 23·0; and subsequent measurements at fairly regular intervals of about 0·3 cm. (total lengths). The spawning season is again in the summer and hence these figures must be taken to represent lengths at rather less than 1, 2, 3, etc. years respectively. There is a good deal of difference between this series and

* Not available to the writer; quoted in De Buen (1937).

that for Brittany, which Hickling (1939) has endeavoured to explain as an effect of selection by the different mesh-sizes used in drift nets on opposite sides of the Channel.

Taking now *Sardinops caerulea,* there are some data with regard to its growth-rate in California. W. F. Thompson (1926, pp. 53-7) made the first attempt to read the scales, but encountered considerable difficulties and later abandoned the work. However, his tentative estimates of length at the times of formation of the first five rings were respectively: 8·0 to 10·5; 14·5 to 16·0; 17·5 to 19·0; 19·5 to 20·5; and 21·0 cm. body length. Walford and Mosher (1943*a*, 1943*b*) have recently made a fresh attack upon this problem, which seems to be proving much more successful, although the results are incomplete. In their second publication they show that the rings are formed at the general winter season (pp. 9-11, 20), and this is apparently intended to supersede the statement in the earlier work (which related to younger fish) that they were formed in the late summer and autumn (p. 10). It appears (1943*a*, Fig. 10) that at the first five winters of life the average sizes attained are respectively about 11·0, 16·0, 20·0, 21·0, and 22·0 cm. body length, and since the spawning season is in the spring (Scofield 1934; Clark 1934) the above-mentioned sizes would probably represent those attained at ages of about $\frac{3}{4}$, $1\frac{3}{4}$, $2\frac{3}{4}$, etc. years. The figures are of the same order as Thompson's but consistently rather higher, and because of the much greater amount of material examined by Walford and Mosher, this second series is to be preferred. The figures can be converted to total length, for comparison with the European results, from information given in a number of places in the California Fish Bulletin series, and on this basis they are approximately 13·0, 19·0, 24·0, 25·0, and 26·0 cm. There is, however, evidence that the fish may live for more than ten years.

For the Asiatic *Sardinops melanosticta,* the evidence is imperfect and somewhat contradictory. Some work on scales has been done by Aikawa (1940) and Yasuda (1940) in Japan, and apparently also by other authors whom Yasuda quotes, but references to whose work are unavailable to the writer. Aikawa believed that there were two age-rings formed in every year, one in the summer and one in the winter, and on this basis his L_2, L_4, and L_6 would correspond to the L_1, L_2, and L_3 of other authors. These figures for the first three winter rings are approximately 11·5, 15·5, and 18·0 cm. *body length.* These can be transposed into the corresponding total lengths from the Californian conversion scale, because Taranetz (1938) was unable to find any significant morphological differences between the two species, and the figures thus become about 13·5, 18·0 and 21·0 cm. The spawning season of the pilchard in Japan is broadly in the springtime (see Kishinouye 1907, p. 81), and so the above series would represent the mean lengths at ages of about $\frac{3}{4}$, $1\frac{3}{4}$, and $2\frac{3}{4}$ years respectively.

However Aikawa's findings were criticized by Yasuda (1940), who, though not presenting any real evidence, believed that, with the exception of the first, all rings on the scales were yearly. Assuming that this means they are all formed in winter, the approximate body lengths for the first five winters would be about 11·5, 13·5, 15·5, 17·0, and 18·0 cm., equivalent to 13·5, 16·0, 18·0, 20·0, and 21·0 cm. total length. Neither of the accounts by these two

authors is at all well documented and the present writer is unable to decide which statement is more acceptable. Kishinouye (1907, p. 85 and pl. XV.) indicated, from what appears to be some kind of study of length frequencies, that the fish attain lengths, of about 12·5, 16·5, 20·5, and 24·5 cm. (apparently total length, since the contrary is not stated) at 1, 2, 3, and 4 years respectively. This estimate of growth-rate is more in agreement with that of Aikawa on the whole.

Finally, Kaganovskaya (1937) gave the following figures, presumably representing total lengths. for L_1, L_2, etc. in respect of pilchards from Siberian waters: 11·5, 15·0, 18·0, 19·0, 19·5, and 21·0 cm. It is not stated at what time of the year the rings are formed, nor when the pilchards spawn in this area, and so it is preferable to ignore this series altogether in any comparison. If the rings were winter rings and the spawning season about the same as that in Japan, the growth-rate would be rather similar to that postulated by Yasuda.

The results of the foregoing review of the literature on the growth of pilchards overseas have been plotted, together with those for the fish of New South Wales as revealed in the present study, in Fig. 7. The New South Wales L_n means have to be transposed into total lengths to render them comparable with the European data, for which the equation is:

$$\text{total length} = 1{\cdot}17 \times \text{body length},$$

and from this the required values for the intermediate lengths are, rounding to the nearest half-cm. in each case as was done for the overseas data, respectively 10·5, 14·0, 17·0, and 19·0 cm. total length. The equivalent figures in inches of total length are approximately 4·2, 5·6, 6·6, and 7·5, referring to ages of about 1¼, 2, 3, and 4 years.

In making the general comparison between the growth-curves, too much emphasis should not be placed upon differences with respect to the first year or two of life. This follows from the difficulties of appraising the real meaning of data on calculated intermediate lengths as between fish which may have spawned at rather different times of the year, even in the same general region; and also from the fact that some workers calculated these lengths from the direct-proportion formula and some did not. For the subsequent intermediate lengths, where the annual increments are less, the general position would not be very importantly affected.

The general conclusion to be drawn is that the growth-rate of the pilchard in New South Wales waters is more like that of the Atlantic coast of Europe, south of Brittany, than of any other group so far investigated. The greater part of the New South Wales curve falls between those which have been fitted to the two alternative series of L values for this Atlantic region. The comparison with the Mediterranean pilchard definitely favors the New South Wales fish, certainly after the second year, regardless of whether the French or Algerian data are considered. On the other hand, the New South Wales pilchard growth-rate is obviously inferior to that of Britain, Japan (regardless of differences between authors), and especially California. The Brittany curve falls somewhat near the New South Wales one, indicating a better growth at first and a poorer one in later life, but the suggestion from Fig, 7 is that the

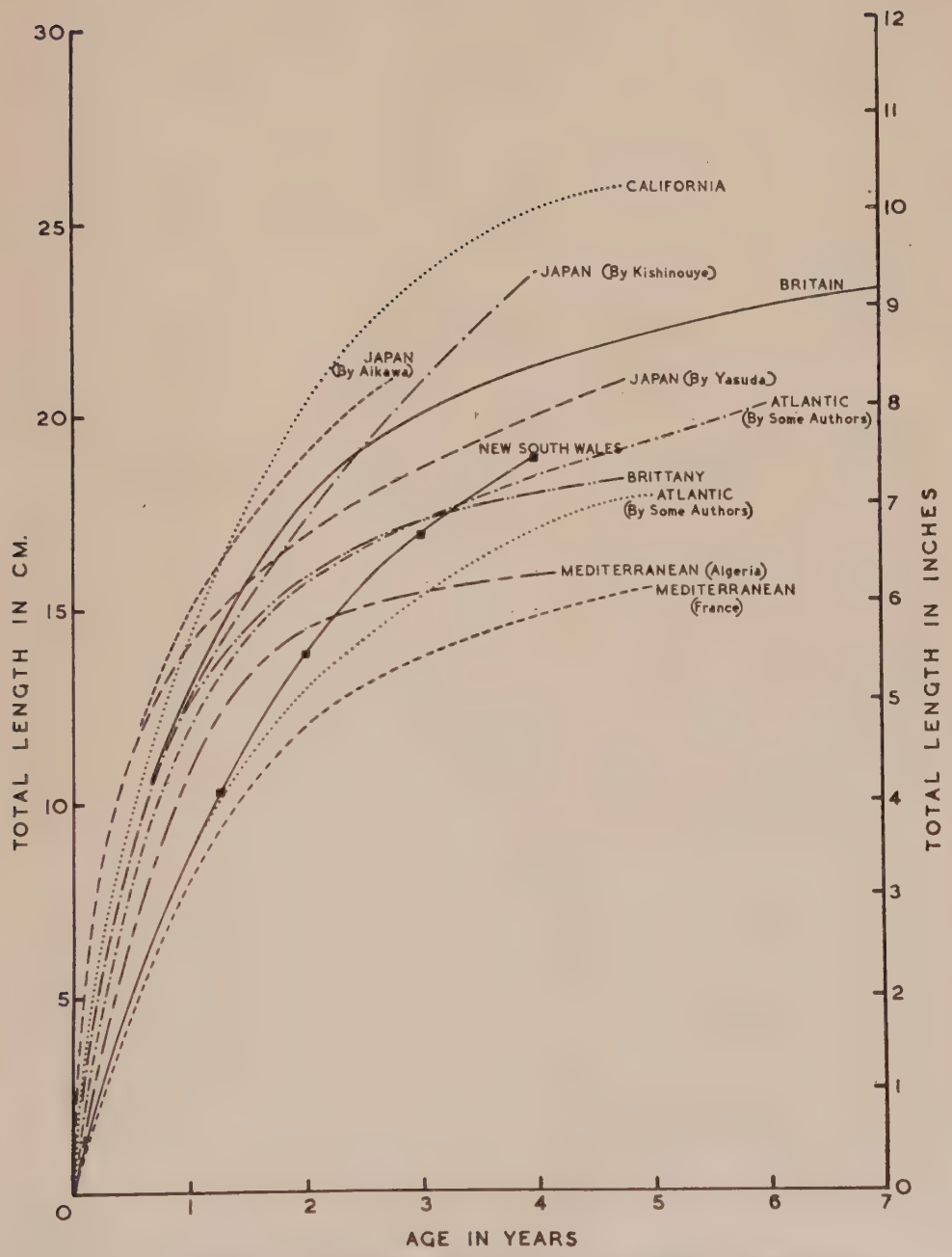

Fig. 7.—Approximate growth-rate curves for the pilchard of New South Wales and related species in Europe, Asia, and North America, from information summarized in the text. (The reference to "Atlantic" signifies the Atlantic coast of Europe south of Brittany.)

greatest similarity to the New South Wales position is revealed by the data for European waters a little further south. The schemes of growth-rate for Brittany and Britain would be open to modification if it could be shown that the annual rings were spawning marks in later life, as they mostly are in the New South Wales material, because of the spawning season being in the summer in these areas. However, any such alterations would probably not greatly affect the present broad comparison.

Summarizing, in respect of its growth-rate the New South Wales pilchard most resembles that of the Atlantic coast of south-western Europe (Spain, Portugal, and southern France). It grows faster than the pilchard of the Mediterranean and more slowly than those of Great Britain, Japan, and California.

VI. SUMMARY OF THE LIFE-HISTORY OF THE NEW SOUTH WALES PILCHARD

Having concluded the study of the age and growth-rate of the Australian pilchard in New South Wales waters, it is possible to present an outline of the general life-history of the species in this area. This draws also upon some of the findings of earlier studies (Blackburn 1941), and upon other information previously mentioned in the present study and some presented now.

In an earlier section (II) it was pointed out that the overwhelming bulk of the smaller pilchards taken in these investigations, i.e. of the 0- and I-groups, was obtained in the spring and summer of the year, whereas a similar proportion of the older fish was secured in the autumn and winter. The source of this information was Table 2, and in this the occurrences are also dissected further, with regard to the kind of environment from which the samples were obtained. Two types of environment were distinguished, the open sea (i.e. neritic waters, since the pilchards do not ever seem to occur importantly beyond the edge of the continental shelf (see Blackburn 1941, pp. 27, 34, 39)) and the bays and inlets. An inspection of the table reveals that the 0- and I-group fish taken in the spring and summer were virtually all from the inlets, whereas most of the older fish of the autumn and winter were obtaining at sea.

From these observations, certain conclusions could be drawn at quite an early stage (they were tentatively indicated in Blackburn 1941, p. 116) and these have been supported by subsequent observations and seem quite securely established. The spawning takes place at sea between the late autumn and early spring, and the larvae hatch there and grow to some 25 mm. of body length (Blackburn, pp. 22, 34-5). Then there ensues a movement of the late larvae and postlarvae in towards the shore, where they enter the more circumscribed bay and inlet waters. At this stage they are of average length about 40 mm. and about four to five months old, so that the season for them may vary from about September to February, according to how early or late they were spawned in the previous general winter season (see section II). At this stage too the young pilchards pass through a large part of the metamorphic phase which seems to apply (Blackburn, pp. 22-3) more or less as described for the European species by De Buen (1930, pp. 186-7). There is a tendency for them to school together and they have often been observed in these formations just below the surface. Furthermore, appreciable numbers have at

times been taken in a single haul of a fishing net. On their way in from the spawning grounds, before they reach the inlets, the young postlarvae are apt to be preyed upon by tunas and other large fishes, and most of the specimens of these stages that were got at sea were actually obtained from tuna stomachs.

During the autumn and winter these young pilchards, now mostly at or approaching their first anniversary of birth, are no longer seen, and it is considered that they become dispersed in various parts of the inlet waters. Considering the great numbers that must be involved, it is perhaps an objection to this hypothesis that they are not reported by estuary fishermen from their beach-seine catches, but it must be remembered that these men habitually do take (and reject from their catches) considerable numbers of small fish of different kinds in which they are not interested, and these might very well include small pilchards at times; also, relatively few fishermen can positively distinguish a pilchard at any stage. Moreover, these small fish would tend to escape through nearly all the mesh-sizes used, and thus might not often be landed at all, and it could also happen that they live in the deeper waters beyond the reach of beach nets. At any rate a few specimens have been procured from these inshore waters in the autumn and winter (mostly with a special fine-meshed seine) whereas the appropriate size-groups have never been found anywhere else, and it is practically certain that they spend the whole of this period in the bays. When one next encounters these fish it is for the most part in the spring and early summer, by which time they are of average age about 1¼ years and of average length about 90 mm., although at this time the size increases very rapidly. These fish are typically congregated into shoals, which are often seen at the surface and are at times quite large, and these shoals constitute the spring run of pilchards on this coast. They are found mostly towards the mouths of the bays, sometimes inside, sometimes a little to sea, and it is clear from this and from their subsequent life-history that at this stage the fish are engaged upon a return to the open sea, after almost a year's existence in the sheltered inshore waters. All the individuals are still sexually immature at this stage.

After about December or a little later these pilchards are not usually seen for a while, but become conspicuous again as surface shoals sometime during the autumn, and are seen from then on for about four or five months, and these occurrences constitute the principal season of the year so far as the surface waters are concerned. The starting and finishing times of the season vary according to locality, being later on the whole as one proceeds northwards along the coast (Blackburn, loc. cit., pp. 38-9). At this stage the fish are found mostly in the open sea, usually from about 2 to 8 miles offshore, and there they seem to remain, for the most part, for the rest of their lives. However, considerable numbers do from time to time re-enter the more open sections of the bays and leave again, in a more or less sporadic fashion. At this first general winter season after their return to the sea the fish have finished their fast growth of the spring and are now growing very little or not at all, having, however, in the meantime increased to an average size of about 120 mm. They are now about two years old and some of them, apparently quite a substantial proportion, have attained sexual maturity. The spawning act must take place below the surface, as nearly all the individuals

in the surface shoals that are not virgins are spent (see Section III, 3). At the end of this general winter season the fish mostly disappear from the surface (but some shoals are apt to be found at almost any season) and are not seen again until the same time in the following year, when they are about three years old. It is not known precisely where they go but it is probably merely deeper down. Such adult fish as may be taken in the general summer season, between the winter runs, are very fat, whereas the fish of the winter shoals are lean and contain little oil, which change is doubtless connected with the reproduction cycle (Blackburn, pp. 44-5)*. There is increased growth between these first and second winters in the resumed sea phase (i.e. the second and third winters after hatching), during which time the fish increase to about 145 mm. on average and then probably almost cease to grow again in the colder months, so that they are approximately of this size at three years of age, when hardly any fish are still virgins.

The same cycle is probably gone through in the fourth year of life, i.e. relatively fast spring and/or summer growth succeeded by very little in the autumn and winter, the gonads in the former period being filling and the body condition good, whereas in the latter season the fish are mature or spent and in rather poor condition. There are indications that food may be more difficult to get in the colder season, because the crustaceans that are mostly eaten are scarcer then. It may also be noted that the relatively few shoals that do occur at the surface in the warmer season (and this applies to the spring run of the I-group also) are more often found at night, whereas the shoals of the autumn and winter, which is the principal surface shoaling season, are commoner by day (unpublished work). At four years the average size is about 162 mm. However, one definite V-group individual was obtained which measured 193 mm., and there have been a few more taken at about this size (maximum 196 mm.) which were probably five or six years of age.† It is not known whether the fish live to any greater age, but some may do so. For Algerian waters Murat (1935, p. 137) noted that whilst the ordinary surface pilchard shoals contain fish up to about four years of age only, individuals of up to eight years are apt to be brought up from below by trawlers.

At any rate it appears that for practical purposes the winter runs of schooling pilchards in New South Wales waters consist almost entirely of individuals of the II-, III- and IV-groups only. Furthermore, it appears fairly certain that the members of the II-group greatly outnumber the older fish. While the samples that have been obtained in these investigations to date certainly do not give a very precise picture of age-composition of the pilchard stocks in the open sea phase, the information already presented here on length-frequency distribution very definitely points to the above conclusion, and a lengthy study of some material collected since 1941 indicates the same. The spring runs associated with the bay waters are mainly composed of I.-group fish only, though even here there may be some association with older fish engaged in a sporadic and temporary inshore migration.

* The yearlings of the spring runs are not oily either (Blackburn, p. 119); this is probably connected with the small size.

† A few more V-group and one VI-group fish have since been recognized in new material.

The foregoing outline of pilchard life-history is more or less complete except from the standpoint of possible major migrations. In the necessary absence of any tagging work the only evidence which could assist in investigating this question would be that in connexion with possible racial differences or lack of them, which might indicate whether the pilchards of New South Wales are assignable to one major stock of individuals intermingling over a large area, or to a number of more local populations of more stationary fish.

This research is in progress now and there are clear indications of at least two communities of pilchards which probably do not intermingle by making very large migrations along the New South Wales coast.

The information just given has been presented in diagramatic form in Fig. 8.

It is of interest to compare this outline with the accounts that have been given of the life-history of other pilchard species. Actually there are only two for which this information is fairly complete, namely the European form (in part) and the North American.

The life-history of the European pilchard has been summarized by De Buen (1937, pp. 406-11), though this account seems to refer more to the winter-spawning populations of south-western Europe than to the summer-spawners of the English Channel and adjacent waters. Although the fish of the former region all spawn at the same general season, it is considered that they probably fall into several distinct populations which occupy their own special areas and do not intermingle over the whole general south-western sector (see also De Buen, pp. 370-5). Thus, although these pilchards may apparently travel considerable distances during their lifetime, they are not to be considered as migratory fish on the grand scale, and the length of coastline upon which any individual population is based would have to be thought of in terms of hundreds. rather than thousands, of miles. The spawning areas, of which there are several, are fairly close to the coast (but further off than in New South Wales) and after hatching the larvae work towards the shore. Arriving there as postlarvae, they go through their metamorphosis and pass the remainder of their first year of life in the inshore waters. After this the fish apparently move about a good deal from place to place in search of food, but are still more or less associated with the immediate coastal waters. During the second year of life most of them become mature, and as they approach their second anniversary of birth they migrate, together with the fish of older age-groups which have also been feeding along the coast, back into the more open waters to spawn. At this stage they often form conspicuous surface shoals. In subsequent years this cycle is repeated.

In Brittany, where the pilchards spawn in summer, Le Gall (1930, pp. 45-6) has established a somewhat different picture from the above. The young larvae proceed towards the shore as before, and spend a few months in the bays and estuaries. However (it is stated) as the first winter approaches they retreat back to sea and go into the deeper waters. In the following summer or thereabouts, when they are yearlings, the fish appear again fairly close to the shore as large masses of immature individuals ("sardines de rogue"). In the winter they seem to move further out again and their gonads begin to fill,

and in the warmer months of the following year they appear more towards the coast again and spawn, at the age of two years, along with the fish of the older age-groups ("sardines de derive"). In subsequent years the cycle of the second year is repeated.

The account given by De Buen, at least, is extremely reminiscent of what has been established in respect of the life history of the pilchard in New South Wales, and there are also some points of similarity here as regards the position that apparently obtains in Brittany. One notes in general for the European species the existence of a number of somewhat local communities of fish, and a number of spawning grounds situated more or less towards the coast, as is the case in New South Wales. In both cases the larvae make for the inshore waters and remain there for some time. More or less similar also is the fact that the European fish mature for the first time at two years and form conspicuous concentrations at that time.

On the Pacific North American coast the general situation is quite different. The facts of the matter have been summarized for the most part by Clark (1940). Here it has been established, mainly from tagging work, that there is but one huge community of pilchards extending along a coastline of over three thousand miles, from northern Mexican to southern Alaskan waters. The areas that serve the entire population as spawning grounds are, however, concentrated towards the southern end of the range, especially just north of the Mexican border.* These grounds extend offshore to about a hundred miles or more, although at most times of their life the pilchards do not occur importantly far beyond the edge of the continental shelf, i.e. not more than about ten miles off the shore for the most part (see also Clark, 1937). The larvae are carried by the currents towards the sandy beaches of the adjacent part of the coastline, and these southern inshore areas function as nursery grounds for the young sardines until they are perhaps as much as a year old. There is some movement between these general nursery areas, the fish tending to work into deeper waters, and along the coast, as they become larger. "In their second summer, if not earlier, they exhibit some northward movement and the extent of this . . . . . increases year by year. The largest and oldest fish reach the waters of British Columbia, Washington, and Oregon. This summer northward migration is followed by a southward return in the fall and winter preparatory to the spring spawning" (Clark, 1940, p. 45). The fishing seasons in the different regions are regulated by these migrations, those in the northern parts of the coast being at about the summer, those in central California from the early autumn through the winter and those in southern California from the late autumn to the early spring, just before spawning begins for the adults. It is thus that the Californians are able to utilize their pilchards as a source of oil on a huge scale, because the fish that are mostly available to them as surface shoals in the shelf waters are those that are in the early pre-spawning stages when the condition is good, whereas when they are really ripe they no

* In a more recent publication (Clark 1947) it is suggested that the position is somewhat more complex than this. There seem to be several populations, possibly arising from a series of nursery grounds all along the coast. However, there is a very extensive intermingling of at least most of these groups, as from an early stage in the life of the fish, and it is probable that some groups make greater contributions to the total stock of the species than others.

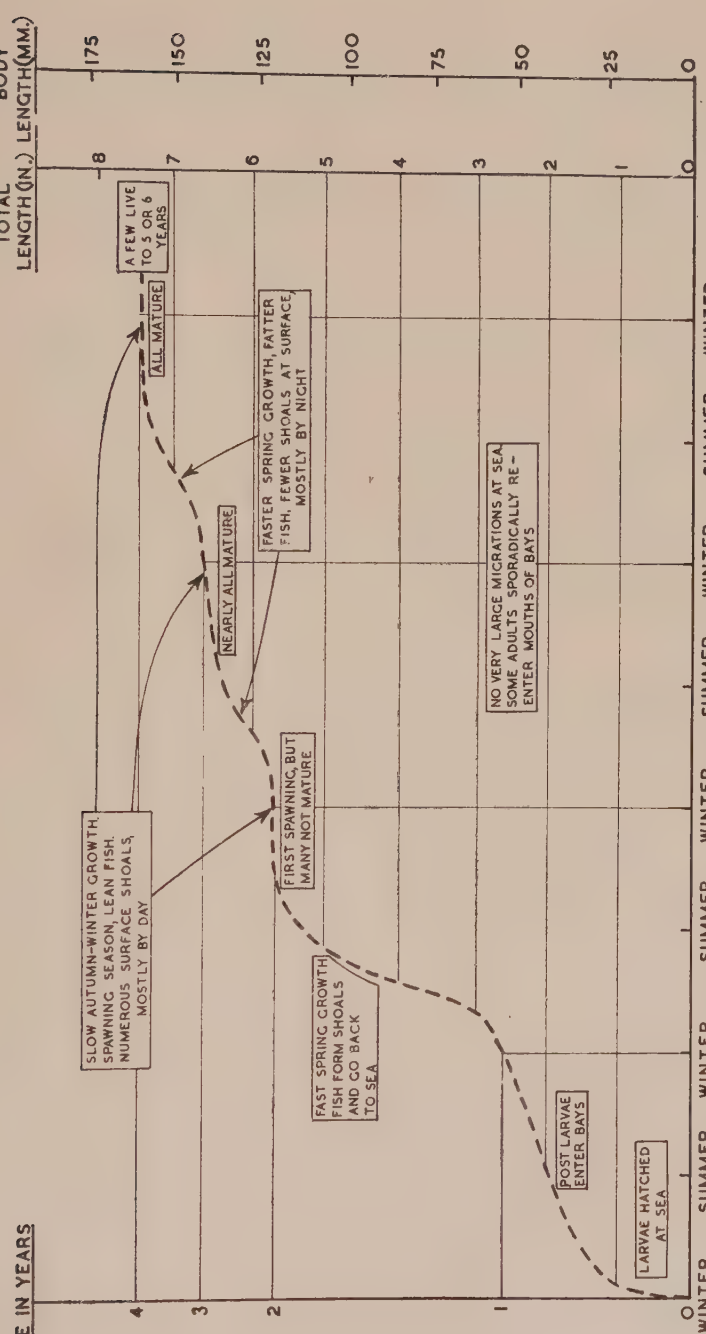
AGE IN YEARS
TOTAL LENGTH (IN.)
BODY LENGTH (MM.)
WINTER SUMMER WINTER SUMMER WINTER SUMMER WINTER SUMMER WINTER
LARVAE HATCHED AT SEA
POST LARVAE ENTER BAYS
FAST SPRING GROWTH FISH FORM SHOALS AND GO BACK TO SEA
FIRST SPAWNING, BUT MANY NOT MATURE
SLOW AUTUMN-WINTER GROWTH, SPAWNING SEASON, LEAN FISH, NUMEROUS SURFACE SHOALS, MOSTLY BY DAY
NEARLY ALL MATURE
FASTER SPRING GROWTH, FATTER FISH, FEWER SHOALS AT SURFACE, MOSTLY BY NIGHT
ALL MATURE
A FEW LIVE TO 5 OR 6 YEARS
NO VERY LARGE MIGRATIONS AT SEA, SOME ADULTS SPORADICALLY RE-ENTER MOUTHS OF BAYS

Fig. 8.—Diagrammatic scheme of the general life-history of the pilchard of New South Wales waters. For further explanation see text.

longer have much oil, just as is found in the Australian and European species*. The fish mature rather late, only a small proportion ripening at two years, about half at three, and nearly all at four. However, this species attains a substantially greater age than the others, with the exception of *Sardina pilchardus* in British waters. There is very little in all this that is much like either the European or Australian pilchard life-history, although again the larvae move towards the inshore waters and remain there for something approaching a year, after which they range further out and over larger areas generally.

The writer is unable to obtain from the available literature any very complete picture of the life-history of the Asiatic pilchard. It is again apparently mainly found within the general coastal waters (Kishinouye 1907, pp. 72-6). In the colder seasons the fish seem to retire from the immediate vicinity of the shore and go also deeper down (loc. cit.), more or less as they are supposed to do in Brittany. Spawning is carried on fairly close to the land and the post-larvae "crowd in the shallow water" (loc. cit., pp. 82-4). Aikawa (1940, esp. pp. 104-11) believed that there are several spawning areas and at least two main populations of these fish in Japanese waters, and that these carry on fairly extensive and involved migrations around the whole archipelago, in the course of which some intermingling of adults of the two groups takes place. All this is not particularly like the situation in any of the other species. Also, according to Kishinouye (loc. cit., p. 85), the fish in these waters attain maturity at the end of one year.

It is seen from all this that the New South Wales pilchard rather closely resembles that of south-western Europe in the general circumstances of its life-history as well as the growth-rate, whereas on both counts there are marked differences between this Australian form and those of North America and Asia. However, the Australian species is much less closely related morphologically to the European one than to the other two, and is also much more distant geographically, and hence it appears as if these likenesses are basically effects of adaptation to environment which must be in many ways somewhat alike. These remarks, of course, have validity for New South Wales waters only so far as the Australian environment is concerned, at the present stage of these investigations.

VII. GENERAL CONCLUSIONS

The main conclusions of this study, so far as the specific question of the age, growth, and life-history of the pilchard is concerned, are as follows:

1. The pilchards of the New South Wales waters belong to the eastern group of this species in Australia, which comprise occurrences on the Queensland (south) coast also. The members of this group spawn in the general winter season. (This conclusion actually relates to previously published work, but is restated here for completeness.)

2. The fish attain an average body length of about 38 to 40 mm. (1·9 inches total length) at about four or five months of age. The size at the end of the first year is not precisely known, but is probably about 55 mm. body length (2·6 inches total length).

* Also the Asiatic form (See Kishinouye 1907, p. 86).

3. At the age of about 1¼ years, in the second spring of life, the average body length is about 91 mm. (4·2 inches total length) and at this general stage the fish are very fast-growing. However, growth virtually ceases throughout the subsequent general winter season, when the fish are 120 mm. in body length (5·6 inches total length) on average, at about two years of age.

4. There is probably a similar cycle in each of the two succeeding years, with faster growth in the spring (and summer) and slow growth in the colder season. The mean body lengths at the end of the third and fourth years respectively are about 144 and 162 mm. (corresponding to total lengths of 6·6 and 7·5 inches).

5. Fish over four years of age seem to be rare, but some live to five and six years. The maximum length recorded in these investigations is 196 mm. body length (9·0 inches total length).

6. The differences in growth-rate between the fish of the north and south coasts of New South Wales, if any, are small, and the indications are that the same applies typically to the different year-classes.

7. As regards the general scheme of life-history, the larvae move inshore from the spawning areas and enter the inlets, where they metamorphose and remain until they are over a year old. The fish then congregate into shoals and return to the sea, where they mostly remain thereafter, though not apparently venturing beyond the edge of the continental shelf.

8. In the open sea phase the pilchards are most conspicuous at the surface in the general winter season of each year, the actual period being progressively later towards the north. These shoals are associated with spawning and the fish are mostly in poor condition, although a large proportion are still unripe at two years and some perhaps at three. In the warmer parts of the year the adult fish are not often found at the surface, but such individuals as do occur are fat. The two-year-olds seem to outnumber those at all higher ages in respect of this phase of life.

9. In respect both of growth-rate and general life-history the New South Wales pilchards more closely resemble those of the Atlantic coast of south-western Europe than those of any other closely related pilchard group studied. These other groups include those of California, Japan, and Britain which have a faster growth, and those of the Mediterranean which have a slower one.

In addition, there are certain conclusions of possible interest in connexion with the general academic study of age-investigations with scales, which are as follows:

10. The corresponding scale- and fish-lengths in the pilchard material are not in direct proportion, although over the greater part of the range their increments are.

11. Great difficulty was encountered because of omitted and secondary rings on the scales, and these cases mostly did not seem to be confined to only certain scales from the same fish. It is considered that secondary rings are secondary in that they register events which only affect a minority of the population, not in that they are adventitious marks that appear on some scales only in the same individual.

12. The principal (annual) age-rings are not all formed at the same season of the year. The first one appears in the spring and the subsequent ones in the winter.

13. There is considerable variation in the lengths of the fish at the time of formation of each age-ring, some fish having consistently greater lengths than others at all such periods throughout life, and in consequence seeming to have a faster growth. This effect is shown to be more apparent than real, owing to the fact that these fish are actually the older individuals of a year-brood, while there is no evidence of compensatory growth.

14. Two main kinds of rings are formed upon the scales, of which one sort is generally associated with advancing sexual maturity in the fish. The other kind includes the first annual rings, the later ones where not obliterated by the subsequently-formed " spawning-marks " in mature fish, and the secondary rings. There is some discussion as to the probable circumstances of the formation of all these rings.

VIII. ACKNOWLEDGMENTS

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In addition, there has been assistance rendered in different ways by a considerable number of members and former members of the staff of the Division, whose names are too numerous to mention. It is desired to thank particularly Messrs. G. L. Kesteven and J. A. Tubb, who made some useful suggestions, and Mr. A. Proctor, who prepared the photographs and supervised the drawing of the text figures.

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PLATE 1

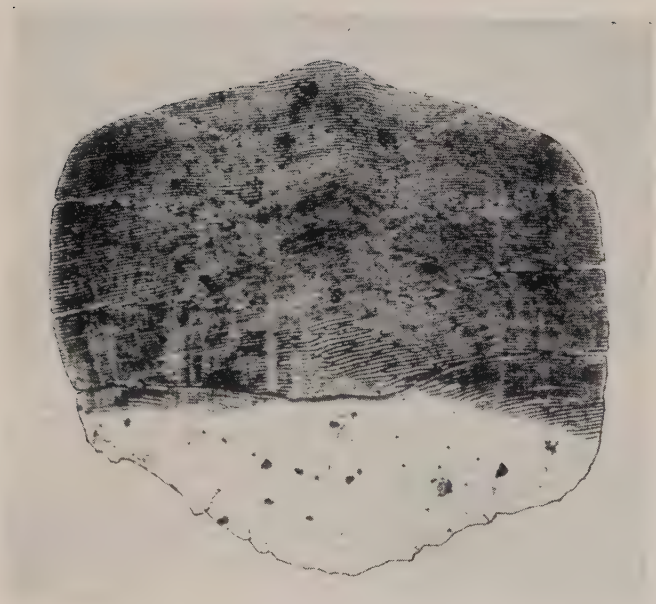

FIG. 1.—Scale, from fish 58 mm. taken in April; no rings.

FIG. 2.—Scale, from fish 89 mm. taken in November; first annual ring present.

FIG. 1.—Scale, from fish 117 mm. taken in June; abnormal first annual ring present, second ring not formed.

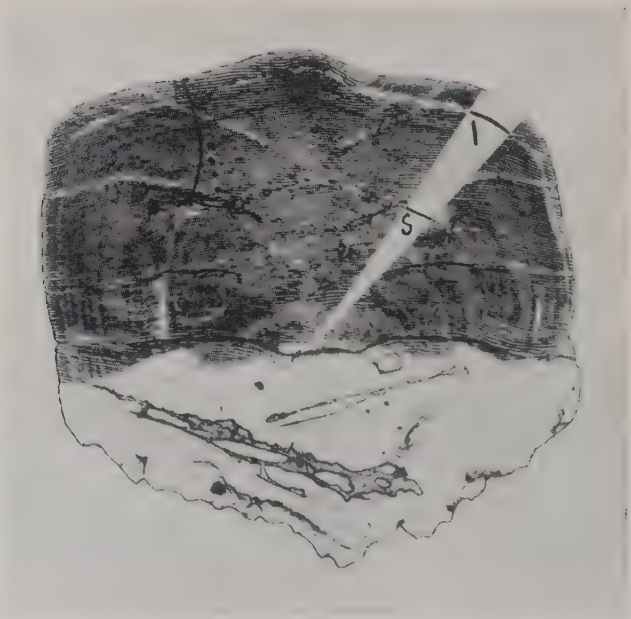

FIG. 2.—Scale, from fish 103 mm. taken in December; first annual and earlier secondary ring present.

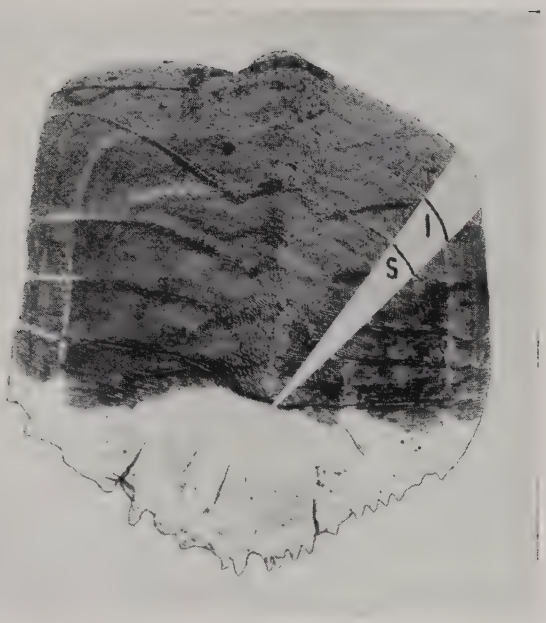

FIG. 1.—Scale, from fish 10·5 cm. taken in November; first annual and earlier secondary ring present.

FIG. 2.—Scale from fish 13·5 cm. taken in June; first and second annual rings present.

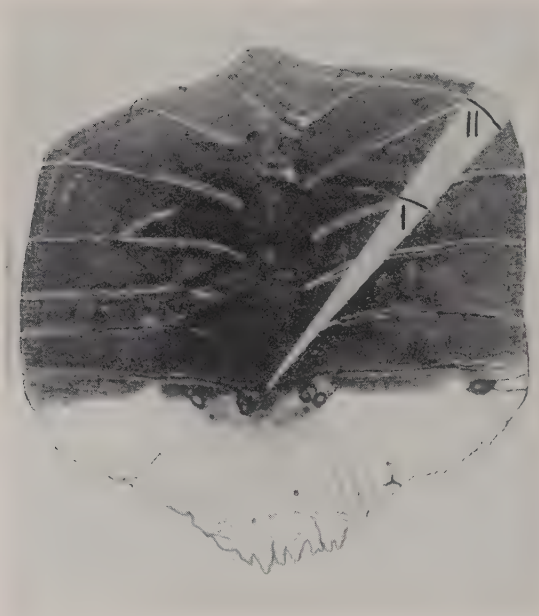

FIG. 1.—Scale from fish 12·5 cm. taken in June; first and second annual rings incomplete.

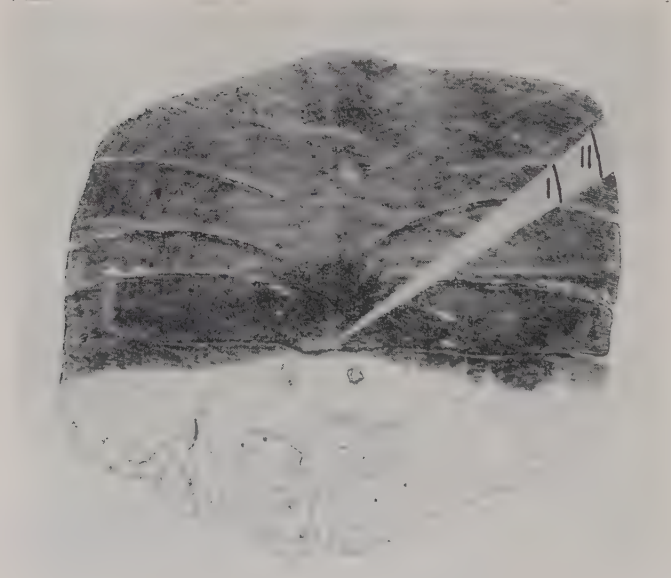

FIG. 2.—Scale, from fish 132 mm. taken in June; first and second annual rings very incomplete.

FIG. 1.—Scale, from fish 128 mm. taken in April; first annual ring missing the second present.

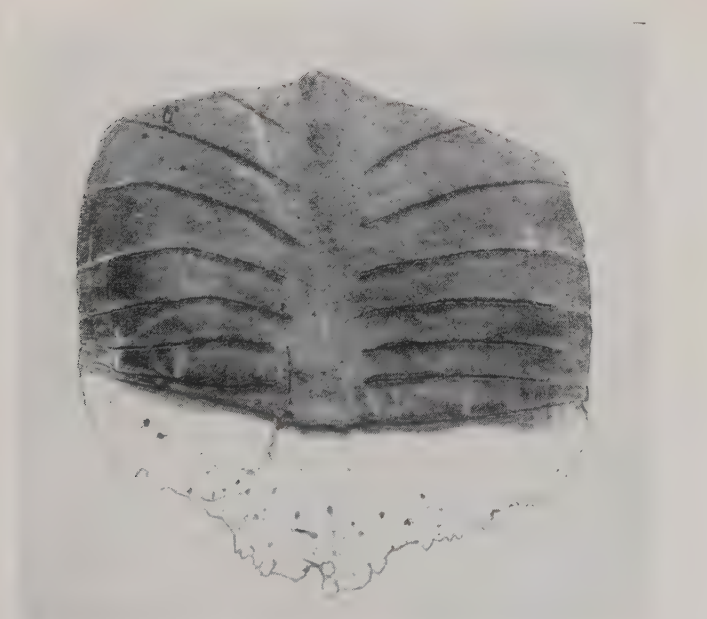

FIG. 2.—Scale, from fish 12·5 cm. taken in May; no definite traces of either first or second ring.

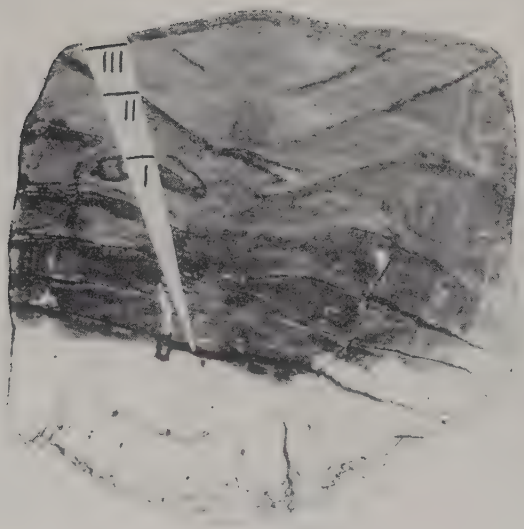

FIG. 1.—Scale, from fish 16·0 cm. taken in August; all three annual rings present, the latter two as spawning marks.

FIG. 2.—Scale, from fish 149 mm. taken in June; first annual ring missing, second and third present as spawning marks, the last with traces of an included yearly ring towards the apex ("casquette").

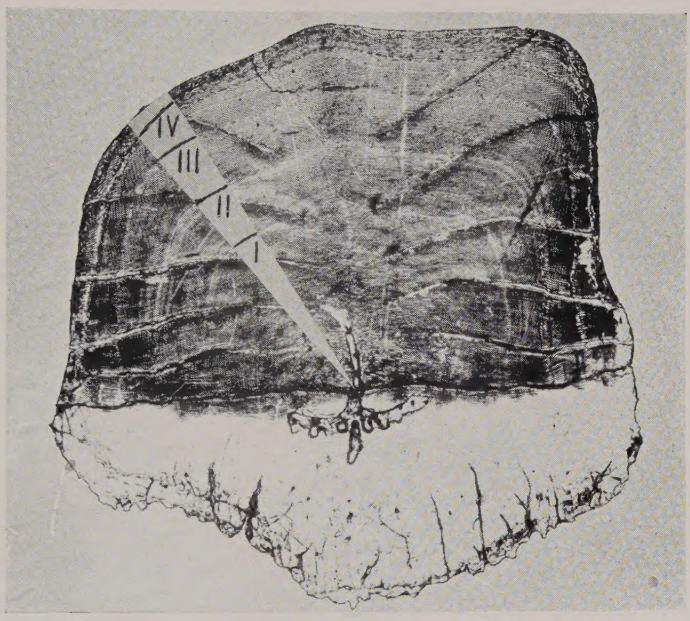

FIG. 1.—Scale, from fish 165 mm. taken in June; all four annual rings present, the latter two as spawning marks, of which the last exhibits "casquette".

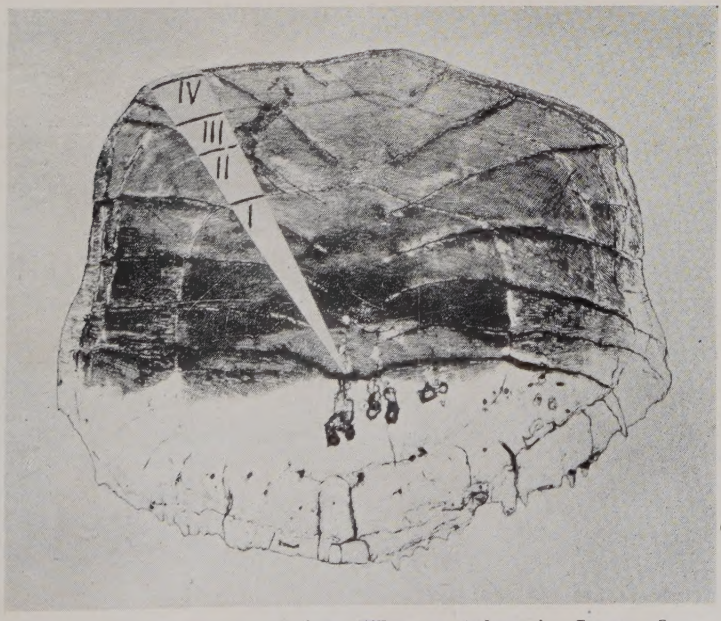

FIG. 2.—Scale, from fish 177 mm. taken in June; first annual ring distinct, second hardly visible, and third and fourth present as spawning marks.

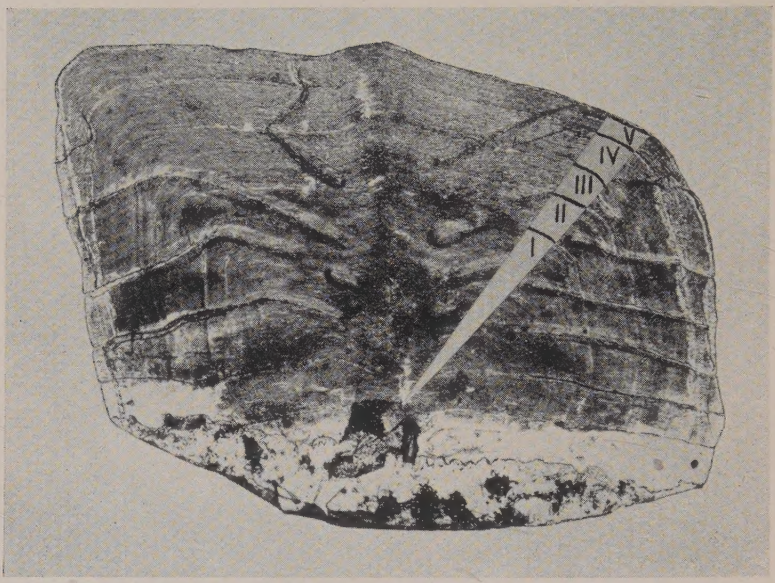

FIG. 1.—Scale, from fish 193 mm. taken in October; all five annual rings present, the latter two as spawning marks.

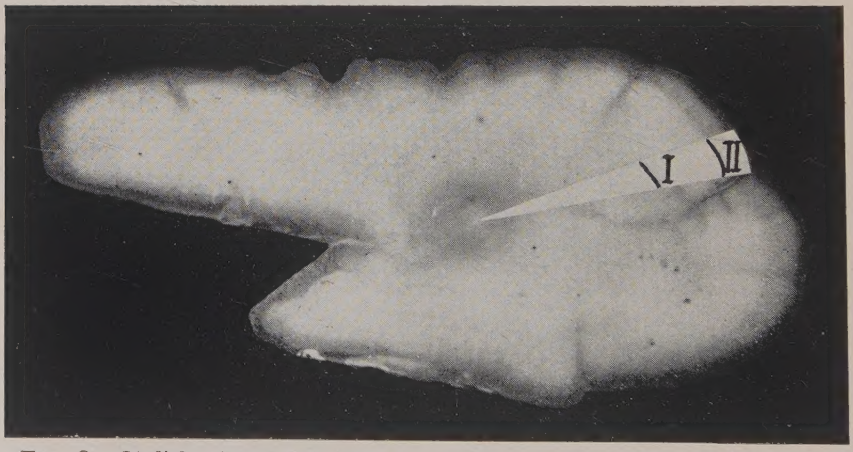

FIG. 2.—Otolith, from fish 11·5 cm. taken in May; first and second annual rings present.

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